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THE HAUSTORIA OF THE ERYSIPHEÆ.

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(WITH PLATES XI AND XII)

HISTORICAL RÉSUMÉ.

THE early literature on the Erysipheæ is of historical interest chiefly. Until the middle of this century the need of exhaustive observations of the phenomena exhibited by plants had not been felt by botanists generally. The study of plant structure as a means of revealing functions had not been established as opposed to the study of structure as a means of revealing relationships in plants. Hence, though the destruction of crops by parasites had been known since the time of the Greeks and Romans, the idea of parasitism had as yet a vague and erroneous definition. By the middle of the century, however, it seems to have been quite generally accepted that parasitic fungi are nourished in some way by their mycelium, "by imbibing juices impregnated with the peculiar principle of the matrix on which they grow" (28). Thus, though this statement was extremely vague, it looked in the right direction. The mildew of the peach, rose, etc., had long been included in lists of fungi by systematists, yet the study of the structure of the fungus had proceeded only to figuring pieces of hyphæ with their conidiophores and conidia. There was little information at hand, therefore, to assist in understanding the nature of a widespread grape disease soon to be produced by one of these Erysipheæ.

Investigation received a stimulus from economic considerations, when, in 1845, a destructive grape disease appeared at Margate, England. Tucker, a gardener there, was led to a study of a mildew on the vines, because the spread of the fungus kept pace with the symptoms of disease. He published the results of his study in the *Gardeners' Journal* of 1847. The mycelium is described as ramifying through the intercellular spaces of the host-leaves and as sending reproductive branches to the exterior through the stomata. Tucker believed the fungus was a parasite on the vines. He was aided in his investigations by Berkeley (**3**) who figured and described the fungus as a new species (*Oidium Tuckeri*). Berkeley repeatedly referred (**4**) to the hemi-endophytic habit of the fungus, and as late as 1886 Worthington G. Smith (**30**) affirmed that the mycelium may sometimes be found on the interior of the leaves. If Berkeley's observations are correct, *Oidium Tuckeri* would seem to be related to Phyllactinia (p. 175) and to be distinct from the American *Uncinula spiralis*.

From England the disease spread to France and appeared at Versailles in 1848 (**9**). By 1851 it had spread all over Europe, causing much distress in vine-producing districts. Losses to owners of vineyards were so great that in France and Italy commissions were appointed to investigate the disease. Independently, Von Mohl (**33**) set for himself the task of determining whether the fungus caused or followed the disease, since Robineau (**25**) had ascribed the disease to an insect. Von Mohl did not record his methods of investigation, except to state that he examined the interior of the fruit under a microscope (**33**, p. 14). In this connection he noted the cracking of the larger grapes when covered with fungus. His search in the interior tissues of the fruit did not reveal the presence of the fungus there, so he concluded that the fungus produced its effects through the epidermal cells. Upon the epidermal cells of the young leaves, flowers, and fruit were to be seen, as soon as the fungus became visible, brown spots, which spread as the fungus spread. Young fruit upon which the fungus appeared did not

reach maturity, but withered and died. He concluded that the fungus was a true parasite on the vines and produced the disease. In 1853 Von Mohl (**34**) attempted a serious study of the weather conditions under which the fungus was able to accomplish such destruction. He examined the infested leaves more carefully and learned that the brown spots on the leaves appeared wherever the fungus was attached. At the brown spots the hyphæ produced irregular outgrowths for attachment, which he called *Haftorgane*. He strongly objected to the belief of Amici (**1**) of the Italian commission, who reported that the appearance of mildew on the vine was a proof of disease in the plant rather than the cause of the disease. This was the opinion also of Léveillé (**19**). Von Mohl cited in support of his proposition that the mildew produced the disease, the opinions of Visiani and Zanardini, of the Venetian commission. Zanardini (**38**) had observed in 1851 the protrusions by which the fungus appeared to attach itself, and called them *fulcra*. Von Mohl credits Zanardini, therefore, with the discovery of these *Haftorgane*. According to Von Mohl (**34**, p. 594) Visiani believed that he had found root-like organs arising from these *Haftorgane* and penetrating into the epidermal cells of the grape leaves. But Von Mohl did not accept Visiani's observations as correct, for he had seen only the surface organs of attachment and supposed they acted as suckers for imbibing nutriment. It seems probable, then, that Visiani was the first to see what we now call haustoria, and in his comparison of them to the roots of higher plants, he was the first to obtain a conception of those functions by which the parasite nourishes itself. Thus, as the structure of the fungus became better known, the general notion of parasitism took more definite shape.

Berkeley (**6**) believed with Von Mohl that the fungus caused the disease, and that the surface organs of attachment, which Frank (**14**, p. 556) has so well named appressoria, were suckers which drew up the juices of the host plant. Indeed, Berkeley (**5**) and subsequently other English writers applied the term fulcra to the appendages of the perithecia, and Berkeley at

least believed that they thereby absorbed nutriment from the leaves (2). Later, however, he wrote, "It is very doubtful whether they extract anything from the matrix" (7).

De Bary (12) seems to have been the first to work out the structure of the haustoria. His contributions to the subject are by far the most important and embrace the most of what is known of these organs. He applied the name haustoria, however, both to the exterior organs of attachment (Von Mohl's *Haftorgane*) and to the absorbing organs of the fungus, which he found within the epidermal cells of the host leaves. Frank (14, p. 556), at a later date, named the *Haftorgane* appressoria, reserving the term haustoria for the real organs of absorption. Of haustoria De Bary distinguished three sorts (12, p. 26): (*a*) *haustoria exappendiculata*, found in Sphærotheca, Podosphæra, and such forms of Erysiphe as have two-spored asci, the haustoria originating directly from mycelial filaments, which show little or no contortion at the points where the haustoria arise; (*b*) *haustoria appendiculata*, the haustorium arising from a somewhat hemispherical protrusion of the hypha, *i. e.*, from an appressorium; (*c*) *haustoria lobulata*, or lobed appressoria. In his Comparative Morphology (11) De Bary defined haustoria as "special organs of attachment and suction," arising in the Erysipheæ, from septate mycelial hyphæ. At this point the hypha is firmly attached to the epidermis of the host and sends the very minute haustorial branch directly through the outer wall of the host cell. Within the cell the branch enlarges into "an ellipsoidal or somewhat elongated vesicle filled with protoplasm, which in *Erysiphe graminis* is branched in a peculiar manner." The description in his Beiträge (12) is more detailed. Up to the point where the haustorial branch within the cell enlarges to form the body of the absorbing organ, the slender branch is apparently thick walled. This is not actually the case, for up to that point it is surrounded by a tube-like offset from the epidermal wall which the haustorium pierces. In cross secton, the neck of the haustorium would, therefore, be represented by a small circle, surrounded by a broad shining ring from the

host-cell wall. At the point where the vesicle begins, this collar suddenly becomes thin and becomes continuous with the outer contour of the vesicle. The diameter of a mature haustorium proved to be approximately equal to the diameter of the mycelial thread. When the vesicle is young, De Bary says it has a very delicate wall, but an old haustorium has a colorless double-contoured wall within which is minutely granular protoplasm, either homogeneous throughout, or consisting of a dense ball in the middle surrounded by transparent granular protoplasm. In cases where the haustorium is extremely old the contents consist of shining, oily masses. Not infrequently, if the epidermis to be penetrated is thick or if the penetrating tube ceases to grow, he observed that the haustorium does not enlarge into a vesicle, but is surrounded by a cone-shaped or knob-shaped protrusion of epidermal wall projecting into the cell. De Bary also examined grapes and grape leaves infested with *Oidium Tuckeri*. He seldom found the haustoria normal in the fruit of the grape, but usually he found only the penetrating tubes surrounded by the cone-shaped ingrowths of the browned host-cell wall extending into the epidermal cells, as just described. Even in cells containing mature haustoria he found no great disturbance wrought in the cell wall, the cell protoplasm, or fluid contents. He frequently observed, however, in otherwise normal cells, that the haustoria are surrounded by thick, irregular masses of protoplasm belonging to the host-cells, which ammonia or KOH would remove sufficiently so as to allow the true haustoria to be seen. Gradually, the browning observed on the exterior of the epidermis spread to the contents of the infested cells, but he did not observe such extreme browning as was described by Von Mohl. It is to be noticed that all of De Bary's studies of the haustoria were made from the surface of the leaves.

Büsgen (10) refers to haustoria in reporting his observations on the effects of chemotropic and other stimuli upon the germinating tubes of fungi. He germinated conidia of *Erysiphe communis* from leaves of *Polygonum aviculare* on slides under cover glasses. In some cases he used sections of infested leaves

in weak nutrient solutions. He was able to obtain appressoria-like organs where the filaments came in contact with the cover glass, but the germinating tubes had a very limited growth and soon perished. His results with the leaves indicated chemotropic reactions in the filaments. As a whole his experiments on the Erysipheæ were not directly successful and they bear little relation to the haustoria themselves. Reference will be made to this paper again in discussing Phyllactinia.

Galloway (**15**) devotes a short paragraph to haustoria in an account of his observations on the development of *Uncinula spiralis* and figures them in much the same way as De Bary. Harper very briefly describes the haustoria of *Sphaerotheca Castagnei*, and he gives but a single figure (**17**). Palla (**24**) has recently investigated Phyllactinia on Berberis and Corylus, but he concerns himself rather with the habit and structure of the mycelium than of the haustoria. For the minute points of structure his methods are inadequate, as he himself intimates (p. 70).

It will be seen from this brief résumé of the literature that the minute structure and especially the development of the haustoria are almost entirely unknown.

METHODS.

Four fixing solutions were experimented with and their respective merits were compared: Flemming's fluid (stronger solution), Merkel's solution, chrom-acetic acid (0.7 per cent. of the former and 0.3 per cent. of the latter), and a saturated solution of mercuric chlorid in 1 per cent. acetic acid. Flemming's fluid proved the most reliable and satisfactory. In those cases in which it blackened the tissues, the sections, after having been attached to the slides, were bleached for twenty-four hours in hydrogen peroxid before staining. Merkel's solution was frequently satisfactory, but it proved hardly as reliable as Flemming's. The other two solutions were far less useful. The sections of leaves were cut 6–7 μ in thickness and were fixed to the slides by the well-known albumen and distilled water methods. They were cleared in clove oil and mounted in Canada balsam.

Some difficulty was experienced in sectioning those leaves which contain large crystals of calcium oxalate, as Corylus and Xanthoxylum, because these crystals frequently caused the destruction of the ribbons. For that reason, the side of the leaf bearing the fungus was usually turned toward the knife in cutting, unless the fungus was amphigenous.

All staining was done on the slide. Wisselingh (**37**) finds in fresh material that chitin is present in many places as one constituent of fungus cellulose. In the Erysipheæ, chitin appears in the perithecia, appendages, mycelium, conidia, and conidiophores. He does not mention haustoria in this connection and finds no characteristic stain for walls containing both cellulose and chitin; congo-red, however, in neutral and ammoniacal solutions, stains pure cellulose intensely, while if chitin is present also, the color is not dark, unless the chitin be transformed to mycosin.[1] Mangin (**21**) found pectin quite generally present in fungus cellulose and employed ruthenium-red as a characteristic stain. Wisselingh (**37**, p. 632) was able to remove the pectin from cell walls containing it. Mangin did not investigate this question and Wisselingh denies the presence of pectin in the Erysipheæ. My own results confirm this view. With ruthenium-red the fungus would not stain at all, though the middle lamellæ of the cells of the host-leaf gave the pectin reaction. The most characteristic staining obtained in the fungus, in the use of congo-red (neutral and alkaline solutions) and methylene-blue (neutral and acid solutions), was an intense staining of the ascus wall in the perithecium. Wisselingh does not mention this as a part containing chitin, and, since the remainder of the fungus seemed to give the chitin reaction by refusing to stain deeply with congo-red, it is possible that the ascus wall is composed of pure cellulose.

The walls of the haustoria do not show any reactions to stains that would indicate that they contain any different material from the remainder of the fungus. Flemming's well-known triple stain, safranin, gentian-violet, and orange-G, proved

[1] He used a modification of Gilson's method (**16**).

very satisfactory. By this stain the nucleoli of the fungus and host are stained red, the chromatin blue, and the ordinary protoplasm orange. Fungus nuclei in the process of division take the violet stain readily, but in a resting condition they possess chromatin in very minute masses. The most of the nuclei shown in the accompanying figures had to be under-stained with violet in order to prevent the over-staining of the host-tissues. The nuclei are represented as containing conspicuous chromatin granules, because in properly stained nuclei the granules are differentiated.

ERYSIPHE COMMUNIS.

Erysiphe communis proved very favorable for study, and since Erysiphe, Sphærotheca, Microsphæra, and Podosphæra appear to agree closely in respect to their haustoria, the fungus on *Geranium maculatum* will be described as a basis for comparison. *Fig. 8* represents such a case as De Bary described. The hypha from which the haustorium originated is not shown, as the mycelium is very easily so far separated from the leaves in the process of fixing and imbedding as to destroy the connection between haustoria and hyphæ, a fact upon which De Bary (**12**, p. 27) and Harper (**17**) comment. The absorbing organ is seen to consist of a slender, proximal portion, the neck, penetrating the epidermal wall of the cell, within which it enlarges into a vesicular, distal portion with a thin wall. On the interior, the vesicle is filled with a delicate, spongy protoplasm differing in no visible particulars from the protoplasm in the mycelium. A mature haustorium always contains one normal nucleus, a fact to which De Bary does not refer. He probably saw it as the "thick ball" surrounded by transparent protoplasm, to which reference has been made. Harper (**17**) for the first time mentions the nucleus in his paper. *Fig. 11* represents the only case I have seen of a haustorium with two nuclei. This haustorium is also septate and such septa occasionally present themselves (*fig. 13*). *Figs. 8, 19*, etc. show in longitudinal section that the ingrowth from the inner surface of the wall of the host-cell

surrounds and accompanies the neck for a distance, as De Bary reported. It seldom extends down to the body of the haustorium, however, and sometimes is absent altogether (*fig. 16*). The collar from the cell-wall is somewhat different from the wall from which it takes its origin, and usually stains little, while the remaining portion stains with safranin intensely. The outer surface of the neck adheres closely to this collar, the outer boundary of which is represented by the middle circle in *fig. 17*.

But *fig. 8* does not represent the usual conditions in one particular. Almost always a mature haustorium is surrounded by a thick, sheath-like layer which, De Bary says, belongs to the protoplasm of the host-cell. It is clear that, by the use of hand-cut sections of fresh or alcoholic material and by a study of the haustoria from the leaf surface, he was not able to make out the structure of this sheath fully. De Bary describes it as an irregular mass; but it is not extremely irregular and is bounded by a very thin membrane of about the delicacy of the plasmic membrane of the host-cell. In *fig. 9*, for example, the middle cell contains an optical section of a haustorium. Within the center lies the relatively large nucleus with its red-staining nucleolus and fine chromatin granules. Surrounding the nucleus is the spongy protoplasm staining orange. The haustorium-wall surrounds this protoplasm. Exterior to the haustorium are the contents of the sheath described by De Bary as belonging to the protoplasm of the cell, while bounding the whole, in contact with the contents of the host-cell, is the delicate limiting membrane of the sheath itself.

The substance of this sheath looks like protoplasm at first glance and stains with orange, but it is not vacuolated like protoplasm. It consists of a dense, homogeneous, finely-granular mass, most frequently gathered into lumps of varying outline, which appear very slightly granular (*figs. 9, 11, 16*). Rosen (**26,** p. 258) observed in *Puccinia asarina*, growing in the intercellular spaces of Asarum, that the branched haustorium was connected with the nucleus of the host-cell in the majority of cases, and either adhered closely to it or entered it with disorganizing

effect. Harper (**17**, p. 664), disagreeing with De Bary, thinks that among the Erysipheæ this peculiar sheath is, as in Puccinia, the disorganizing nucleus of host-cell. The delicate bounding membrane would, therefore, be the nuclear membrane.

I have not found evidence of such a relation between haustorium and host nucleus in the Erysipheæ. In the examination of many sections in searching for stages in the development of the haustoria, it becomes more and more clear that the host-nuclei and haustoria are indifferent to each other. The sheaths are present around the haustoria even if there are several infesting one cell, as frequently happens. In such cases, if the cell is not so full of haustoria as to obscure the cell contents or crowd the nucleus, that body can be seen in a more or less normal condition. In the cells of hairs which are large enough to contain several haustoria easily, the sheath of each can be seen, while the host-nuclei occupy distant positions in the cells. The sheaths are to be accounted for in another way, as will be shown subsequently.

In most of the figures the host-nuclei lie at a greater or less distance from the haustoria. When, as in *fig. 16*, the connection between the two is close, the nuclei are more or less disorganized. But the cases figured make the proportion seem much too large to be in accordance with the facts. The sheath is not usually bounded by a tensely stretched membrane (*fig. 7* represents a special case), but by a membrane having a more or less irregular outline in section, beginning where the cellulose collar stops. The orange-staining contents are usually present in more or less abundance, except in *Erysiphe graminis* on Poa, where only the sheath is present and is sometimes inconspicuous.

The outer walls of the epidermal cells have an affinity for the safranin stain, but the collar about the haustorium neck stains much more delicately with it. In *fig. 10*, shown because the cell was plasmolyzed, the collar is distinct from other parts and appears under the microscope very slightly stained with safranin. Again (as in *figs. 16, 21*, and frequently in other figures), the reaction is such that the neck of the penetrating organ is

distinctly visible and its slenderness appreciable; whereas, if it were not for this circumstance, the size of the tube would frequently be exaggerated.

Nordhausen, in experimenting with Botrytis, Penicillium, and Mucor (**23**, p. 38), observed a marked browning of the epidermal cells in contact with the germinating spores, which always preceded penetration. He thinks (p. 7) that the phenomena of browning and subsequent death of the cells are due to the production of some poison during the germination of the spores. Von Mohl (**34**, p. 592), De Bary, Frank (**14**, p. 556), and others mention this browning in the Erysipheæ. In the stained sections this brown color is not distinguishable, though the cell wall around the point of penetration is more or less altered and dissolved. Seen from the outer surface of Poa (*Erysiphe communis*) and Eupatorium (*Erysiphe Cichoracearum*), there is an area surrounding the point of penetration which is entirely colorless, clear, and shining. The remaining portions of the epidermal wall stain with safranin. The outer surface of the colorless area is usually depressed also, the depression being deepest at the point of penetration, as though a part of the cellulose had been dissolved away. This dissolution of the cellulose suggests that the Erysipheæ probably produce an enzyme suited to this work.

In the sections of Geranium leaves the safranin stain frequently makes evident the beginning of penetration. The first intimation of the process is a deep staining of the inner surface of the outer wall of the cell immediately under the point where the hypha comes in contact with the epidermis (*fig. 1*). This staining, however, is to be seen occasionally at the cross-walls of the epidermis, where haustoria have never been produced. It is possible that it is this deeply staining spot which shows the brown color in fresh material.

The next step to be observed in the development of the haustoria (*fig. 2*) is the thickening of the epidermal wall toward the interior over an area coinciding roughly with the clear space already mentioned (*fig. 17*). Nordhausen (**23**, p. 17) observed

a slight swelling of this kind with Botrytis on Tradescantia, Mnium, etc., but Ward (**35**) observed with the same fungus (apparently), which produced the lily disease he described, such an extraordinary swelling of the walls of the host that a large part of the lumen of the cells was filled. Nordhausen believes that Botrytis lives on the protoplasm of the poisoned cells chiefly. Ward is of the opinion that the fungus causing the lily-disease lives also on the gelatinized walls. Erysiphe appears to produce not so much a swelling of the wall of the cell as the addition of new material to its inner surface, for the collar of the haustorium, formed from a part of this thickening, is dense and remains as a permanent structure in the cell.

At the same time that the wall of the cell is thickening, growth of the penetrating tube is proceeding. Its distal end enters the wall, and, just at the point where the reddening of the wall originally appeared (*fig. 2*) a very slight enlargement of the tube occurs, accompanied still by the reddening on each side (in longitudinal section). But this effort does not bring the point of the tube into the lumen of the cell, for the thickening of the wall keeps pace for a time with the growth of the tube. This tube is extremely minute. For Botrytis Nordhausen (**23**, p. 39) found it to be one fourth of the diameter of the ordinary hyphae. Miyoshi (**22**)[2] has shown that the membrane to be penetrated affects the size of the tubes. Thus, when collodion was used for a membrane, the tubes actually increased in diameter, while with an onion skin there was no change in the size of the tube. Ward's observations on this point agree with Nordhausen's. In all of the Erysipheæ the tube is much smaller, as the figures show, and it is interesting to note that the nucleus of the absorbing organ must in some manner make its way through this minute passage.

The tube (*fig. 3*) continues its growth through the increasing or (as Ward thinks for Botrytis) swelling cellulose, a part of which remains permanently encircling the neck of the mature

[2] Die Durchborung von Membranen durch Pilzfäden. Jahrb. f. wiss. Bot. 30: 280. 1895.

haustorium as the collar so frequently mentioned. De Bary (12 p. 26) probably saw something of this phenomenon in the form of the knob-shaped papillæ in the cells as mentioned above. He saw the structures in cells with thick epidermis and in what he thought were no longer growing haustoria. Because of the closely connected series of stages which it is possible to secure, it is evident that these are not old, disintegrating haustoria. Rather they represent the early stages of penetration. At any rate, if they represent dead haustoria, they reveal the outlines of the cellulose parts none the less, and so tell the story of development. Just what significance there is in this thickening of the host wall cannot be conclusively determined without experiment. The wall increases not only in bulk, as Ward found, but in quantity, as has been mentioned. That there soon *does* appear to be a disintegration of a portion of this ingrowth, will be seen presently. There are not data at hand to determine whether the penetrating tube, by means of some chemical substance, excites the cell protoplasm to unusual activity in the production of cellulose over the region of penetration, or whether microscopically small needles would cause such a production mechanically. Again, it is possible that the stimulating agent is the atmosphere acting through the wall at the point made thin by the work of the fungus. There would then be the same reason for this local thickening as there was for the original production of a thick outer wall in the first place.

Soon the tube, growing with increasing rapidity, overtakes the cell in what may be its efforts to protect itself from injury by the fungus. Whatever may have been the stimulus which produced it, the thickening of the wall ceases after a considerable ingrowth, U-shaped in outline, has been formed. The first appearance of disintegration is now to be seen in it. The distal end no longer has the appearance of cellulose such as is found in the cell wall and in the clear basal portion. Some change has been wrought in it which has altered its appearance and its reaction to stains. This end (*fig. 4*) may now be stained slightly orange, and it is slightly and minutely granular. No

sharp boundary separates the proximal from the distal end. The granular character of the latter gradually lessens toward the dense proximal end, which stains very slightly with safranin. The still slender penetrating tube is to be seen piercing this basal portion and extending into the now disintegrating distal extremity. It is to be observed that the plasmic membrane of the cell, by means of which the ingrowth has been formed, passes up the side and over the end of that structure. The gradual disintegration of this ingrowth of cellulose thus forms the early stages from which the true structure of the haustorium sheath can be understood.

The growth of the haustorium now continues with accelerated speed. It will be seen in *fig. 5* that the penetrating tube has taken a straight course through the cell wall and the basal portion of the papilla, for a distance approximately equal to the length of the collar in a mature haustorium. From that point on to the point where its growth was checked by the fixing fluid, the tube has pursued a rather tortuous way or else the distal surface of ingrowth has offered some resistance to the progress of the tube. The end of the tube has begun to enlarge into the vesicle which forms the body of the mature haustorium. The nucleus has not yet started in. The whole distal portion of the cellulose surrounding the end of the tube is now distinctly granular and takes a deep orange stain. The staining of the wall on the line of its original inner surface is no longer visible. The hypha from which this tube originated is sufficiently enlarged and flattened to fall within De Bary's class of *haustoria appendiculata*, peculiar to forms of this genus possessing two-spored asci. *Erysiphe communis*, however, would be a species without appressoria, according to this classification.[3]

[3] It seems questionable whether much dependence can be placed upon forms of appressoria in systematic determinations, such as the separation of *E. Galeopsidis* from *E. Cichoracearum* (Ellis and Everhart, N. A. Pyrenomycetes 14. 1892). The former is supposed to have lobed appressoria. The varieties of *E. Galeopsidis* used in this investigation do not appear to show more conspicuous appressoria than *fig. 5* represents. Between the appressorium and the epidermal wall is drawn in outline a cushion-like structure which stained red. This was the only case of the kind observed, and its significance is unknown. In *fig. 5* again the nucleus of the host is on the basal wall of the cell.

In *fig. 6* the absorbing organ is in a thick-walled epidermal cell in the region of the midrib of the leaf. The vesicle has continued to enlarge until it has reached the form, but not the size of a mature haustorium. It would never have possessed the usual sheath, because by pressure or fermentative action, or by both, it has escaped from its enclosing cellulose, which has approximately the same structure as the disintegrating papilla shown in *fig. 5*. The collar at its base, therefore, consists of the entire ingrowth and not of its basal portion only, as is common in most mature haustoria. It does not as yet contain a nucleus. Outside of the cell is shown a piece of mycelium containing numerous safranin-staining bodies which are probably food material of some sort.

In *fig. 7* is shown a nucleus making what appears to be an unsuccessful attempt to enter the haustorium. The hypha has been broken away so far that none of the pieces lying above the cell could be identified surely as belonging to the haustorium. The nucleus seems to find some difficulty in entering, either because of its size or, possibly, because the darkly staining material lying in front of it offers some resistance to its progress. The passage of the nuclei into the haustoria is naturally most difficult to see. This unsatisfactory example is the only case observed. The haustorium must attain nearly its full size, therefore, before it is provided with a nucleus. Up to this time it contains only highly vacuolated protoplasm. It is difficult to find cases which show nuclei in position to pass down the penetrating tubes into the haustoria. The few cases observed have been figured, but it cannot be said conclusively that these are the nuclei which were ultimately to find their way into the haustoria. The nuclei of the hyphæ are sometimes greatly elongated and narrowed (*fig. 14*). It must be in such a form that they make their way into the tube.[4] *Fig. 7* is instructive in another respect. The sheath of the haustorium contained, when the material was fixed, nothing but fluid. The contents have been entirely consumed. But the bounding membrane is

[4]See also figures by Harper, 17, p. 663.

stretched and turgid, and none of the solid contents of the host-cell approaches nearer to the haustorium than the outside of this *sheath-membrane*. That this membrane is so tensely stretched shows that it was filled with a liquid when the material was fixed. It, therefore, possessed osmotic qualities similar to the plasmic membrane of the host-cell. It has been mentioned that the plasmic membrane of the cell, by the activity of which the cellulose papilla was produced, extends over the papilla (*fig. 4*). In *fig. 7* this plasmic membrane is stretched and enlarged extraordinarily until its origin would not be easily recognized.

From what has been said on the development of the haustoria, it is easy to understand the nature of the sheath around the haustorium, with its bounding membrane. That is, it does not belong to the protoplasm of the cell as De Bary supposed, nor is it the host-nucleus as Rosen observed in *Puccinia;* but the contents of the sheath consist of disintegrated cellulose from the distal end of the cellulose ingrowth through which the haustorium has made its way. The bounding membrane of the sheath, on the other hand, is the plasmic membrane of the host-cell stretched and greatly enlarged by the osmotic forces involved. In so far only does the sheath belong to the protoplasm of the cell, and not at all in the sense which De Bary had in mind. There is abundant evidence from various sources to support the view just stated. Marshall Ward (**35**, p. 356) has shown that Botrytis produces a swelling and gelatinization of the cell-walls of the lily leaves. Ward found that the fungus was able to live on this disintegrated cellulose. It is well known that certain fungi produce ferments which are able to digest cellulose. Ward found such a ferment in Botrytis (pp. 343–346). So also Beyerinck (**8**) found that *Coryneum Beyerinckii* makes use of a dissolving ferment. Nordhausen (*l. c.*, p. 38) has shown that Botrytis, Penicillium, and Mucor can enter a cell-wall and grow through it parallel to its surface for comparatively long distances. Indeed, this power of disintegrating cellulose is probably generally possessed by fungi, parasitic and saprophytic. The Erysipheæ probably have such a ferment. The partial

dissolution of the epidermal wall of the host about the point of penetration has been mentioned. The penetrating tube makes its way through a long ingrowth of cellulose before it expands into a mature haustorium. The mature organ shows no unmodified host-cellulose surrounding it except the collar around the neck of the haustorium. The distal portion of the ingrowth partially disappears in the development of the penetrating tube. During the disappearance, it undergoes changes which materially alter its microscopic appearance as concerns structure and its capacity of reacting to stains. It becomes decidedly granular and takes an orange stain, whereas, in the beginning, the entire ingrowth was of the same consistency as the collar, and took the safranin stain slightly. By the time the penetrating tubes begin to enlarge, these changes are conspicuous. The tube may finally break through the cellulose and develop without any sheath. But usually some of the cellulose remains as the granular masses of the sheath. It will be shown subsequently that, under certain conditions, the haustoria of *Uncinula Salicis* have no sheaths, and the sheaths of *Erysiphe graminis* on Poa do not show any contents in the older stages nor are the sheaths always present.

The extremely minute size of the penetrating tube has been mentioned. The amount of fermentative action, of which the young haustorium is capable at first, is, therefore, only sufficient to provide for the onward growth of the tube. The cell succeeds in laying down cellulose ahead of it for a time. The circle of the fermentative effect has not at first a long radius. The distal end of the ingrowth is the first to show signs of dissolution. It becomes granular there. As the absorbing organ attains larger growth the digestive powers of the fungus become more effective, and that part of the collar coming within the sphere of influence of the ferment is gradually attacked and partly dissolved.

It is interesting to find that the membrane by which the sheath is bounded in a majority of cases is contributed from the plasmic membrane of the host-cell. The plasmic membrane is

not ruptured by the ingrowth of cellulose. Rather the ingrowth is caused by the activity of the membrane, the area of which enlarges with the thickening of the wall. The plasmic membrane is still recognizable when the haustorium begins to enlarge at its distal end. It still maintains its osmotic properties at the stage represented by *fig. 7*. In most cases it remains bounding the masses of disintegrated cellulose which constitute the contents of the sheath. *Fig. 7* represents the membrane stretched and firm from the osmotic forces at work in the nutrition of the fungus. At a later stage it usually suffers injury and sometimes dissolution.

This fungus is not capable of producing the extraordinary dissolution of cellulose which Ward found in the case of Botrytis. Its supply of enzymic material seems to be limited. The sheaths are, therefore, usually present, though on rare occasions they are not, as in *figs. 8* and *12*. Certain haustoria of *Uncinula Salicis* do not possess sheaths and, as will be seen, this species has a greater digestive capacity. Nordhausen (**23,** p. 23) found in infecting leaves with spores of Botrytis that heavy dews so weakened the enzyme of the fungus that penetration was impossible. It seems probable that, when the cell-sap of Geranium begins to be absorbed by the young haustoria of Erysiphe, the enzymic material is weakened or largely reabsorbed. Thus it can be seen how the sheaths with their bounding membranes are possible and how, as De Bary observed long ago, the host-cells may escape with so little injury. From the time when the haustoria begin to absorb actively, the further digestion of the cellulose papillæ largely ceases, and though their bounding membranes collapse, they are usually not completely digested, being protected by the cell-sap. In *fig. 8* the sheath is all digested down to the collar. In *fig. 19* the haustoria succeeded in penetrating the wall of the hair, of which the cell forms a part, before the plasmic membrane could build up papillæ to impede the progress of the tubes. The digestive capacity of the haustoria is not entirely constant, so that we find sheaths in various stages of disorganization.

ERYSIPHE GRAMINIS AND OTHER SPECIES.

The absorbing organs of *Erysiphe graminis* on *Poa pratensis* deserve description. It has long been known that the haustoria of this species are "branched in a peculiar manner." This fungus grows very luxuriantly on the grasses and fills the epidermal cells full of large branched haustoria. A shining, colorless area occurs around the penetrating tube (*fig. 17*) which is slightly larger than in *E. communis*. The colorless area is slightly depressed, as already mentioned. The collars of cellulose are relatively thick also. *Fig. 19* represents nearly the maximum thickness for the collars in Poa. The body portion of the absorbing organ is always approximately cylindrical or ellipsoidal, with finger-like projections growing out from the ends or sometimes from only one end (*figs. 19, 21*). A large nucleus lies near the middle, and in either end, in mature examples, there is a large vacuole. The branches are also vacuolated. The body is not always symmetrical with respect to the neck (*fig. 20*) but the neck may be near one end from which, even then, branches may arise. The development of the haustoria of this species was not followed, but in none of the mature examples have the sheaths possessed any granular contents as found in *E. communis* and elsewhere. The sheath-membranes are usually present, though they exhibit great irregularities. Sometimes they are not to be seen except for a short distance; sometimes they completely surround the haustoria, being discernible even down between the branches, At other times the branches penetrate the sheath. The protoplasmic contents of the epidermal cells are usually scanty. It seems impossible that the cell nucleus should escape destruction when the haustoria are thus provided with long branches. But the same indifference to the nucleus exists here as in *E. communis*. Even when a cell contains several haustoria, the nucleus is usually unmolested, and is often as normal in appearance as in uninfested cells. This form of absorbing organ may be looked upon as the result of a special effort of this species to obtain abundant food. The heavy growth of mycelium and the immense number of conidia produced by this species

show the success it has attained. Many of the appressoria of this species agree with De Bary's *haustoria appendiculata*. *Fig. 19*, being a side view, shows only one outline of the organ of attachment. Long infested blades of Poa show signs of injury from the fungus. "In California it has been destructive to wheat" (**13**).[5] Certainly these haustoria give the impression of activity not gained from other Erysipheæ.

The habit or structure of the other species of Erysiphe studied do not differ so much from the account given of *E. communis* that a detailed description is necessary. Basal (and even higher) cells of hairs are especially favorable places for the study of haustoria. *Fig. 16* represents such a cell from a hair of *Eupatorium perfoliatum* infested by *Erysiphe Cichoracearum*. The nucleus of the cell lies between two of the haustoria and seems to be disorganized. The cell is slightly plasmolyzed. The dark globules (stained red in the sections) do not seem to be degeneration products due to the action of the fungus, for the cells in uninfested leaves contain them. They are probably due to the fixing reagents. This plant, it is well known, contains a volatile oil and a resin. It is probable that the globules are related to these substances. It is very common to find such products as these in the autumn, when this material was gathered.

UNCINULA SALICIS.

Uncinula Salicis on *Salix discolor* exhibits peculiarities in its appressoria and haustoria, which apparently have not been reported heretofore. De Bary (**12**, p. 27) mentioned the lobed appressoria (*haustoria lobulata*) of this species, then called *U. adunca*, but he did not report any peculiarities in the haustoria; and Galloway examined *U. spiralis* (*U. necator*). It has frequently been stated by De Bary and others (**12**; **32**; **36**; **20**; **18**; **14**, p. 555; **13**, p. 2; **19**) that the Erysipheæ always confine their absorbing organs to the epidermal cells of the host. Berkeley, it has been mentioned, believed in the hemi-endophytic habit of

[5] The writer has never found it difficult to collect material, with ascospores developed, in August and September.

some of the powdery-mildews, and Palla (**24**, p. 68) has recently shown that Phyllactinia has intercellular hyphæ. *Uncinula Salicis* also offers a striking contradiction to that old conception, but the method by which this fungus reaches the interior tissues of the leaves is different from the one Phyllactinia employs.

Uncinula is amphigenous on the leaves of the willow. Its appressoria are lobed, as De Bary affirmed. The mycelium is entirely external. On the upper surface of the leaves the lobed appressoria give rise to penetrating tubes which enter the epidermal cells. All of these tubes do not develop in the epidermal cells into haustoria. An examination of a cross-section of the willow-leaf shows that the epidermal cells are very abundantly infested with haustoria, but in addition, numerous slender bars can be observed reaching from the outer walls across the epidermal cells to their inner walls. The bars give the cells the appearance of possessing trabeculæ. The haustoria in the cells frequently hide the outer end of these structures, but in following their course to the inner wall, haustoria may sometimes be observed in the palisade cells of the leaf. The bars are the penetrating tubes, or the necks, of these subepidermal haustoria. When the penetrating tubes reach the palisade cells they enlarge into haustoria not unlike the ones described for *E. communis*, possessing the sheaths and nuclei. Several tubes may pierce the outer epidermal wall close together and take different directions across the cells. Of the tubes which penetrate the outer wall of the epidermal cell close together, some may enlarge immediately into haustoria, while others may pass to the palisade cells. This crowding and confusion makes it difficult to discern the true structure. At first glance it looks at times as if the short necks of the epidermal haustoria give rise to one or more branches which develop into haustoria. The deception arises from the crowded position of the organs.

On the under side of the leaf the epidermal cells are likewise penetrated by the slender tubes, some of which immediately enlarge into haustoria, and some of them (a little less than half), penetrate into the mesophyll cells immediately under the

epidermal cells. *Figs. 22–26* all represent cells on the under side of the leaves. The upper epidermal cells of the willow leaves in autumn are so filled with deeply staining products as to make the cells of this epidermis unfavorable for study.

As far as they have been observed the haustoria of *Uncinula Salicis* are not occasionally septate as in *Erysiphe communis*. In the possession of a single nucleus, surrounded by spongy protoplasm, and in its general shape, the haustoria of Uncinula are not peculiar. The subepidermal haustoria are also surrounded by sheaths such as *Erysiphe communis* has. But in the epidermal cells the sheaths are very frequently absent. The explanation of this absence of sheaths lies in the fact that Uncinula is capable of greater enzymic activity than Erysiphe, so that the sheaths are dissolved away. But by the time the tube has penetrated a palisade cell its supply of ferment is either exhausted or weakened (or both), so that the sheaths remain. The typical collar may sometimes be seen around the necks of the haustoria (*fig. 23*), but for the subepidermal haustoria it can be demonstrated at times, from the size and reaction to stains, that the penetrating tube is accompanied entirely across the epidermal cell by the cellulose ingrowth from the outer wall (*figs. 22, 24*).

De Bary does not mention the fact that the lobed appressorium of Uncinula may give rise to several haustoria (*figs. 22, 24*). Other appressoria, as far as they have been observed, produce absorbing organs singly, but on the willow leaf two or more tubes from the same appressorium pierce the epidermis close together. The confusion and crowding of haustoria in the cells is due to this fact, rather than to the fact that the extremely dense mycelium sends many single organs into the leaf. On the other hand, the lobed character of the appressoria seems to be produced by the contortion of the filaments necessitated by the origin of several haustoria in one place. The significance of the term appressoria consists in the fact that the expansions of the filaments which rise to haustoria are commonly closely appressed to the surface. But this habit is not uniform in *Uncinula Salicis*. *Figs. 23, 25*, and *26* show that the appressoria may stand at some

distance from the surface of the host, and the penetrating tubes may have a shorter or longer course before they pierce the cells. Whether such appressoria have been forced away from the surface of the leaves by the resistance offered to the elongating penetrating tubes by the epidermis is not known.

It might be supposed that, where an intercellular space occurs between two subepidermal cells, the penetrating tube might find its way into the interior of the leaf. The haustoria of Uncinula, however, have not been found deeper than the subepidermal cells.

PHYLLACTINIA.

Palla (**24**, p. 68) has recently reported that Phyllactinia[6] has the very interesting habit of sending nutrient hyphæ through the stomata into the intercellular spaces of the infested leaves. Haustoria are thus constructed entirely on the interior of the leaf[7] and are not found in the epidermal cells as in Erysiphe. Because of this unusual habit Palla suggests the separation of the powdery-mildews into two families, the Erysipheæ and the Phyllactineæ. Upon the ground of certain differences, chiefly in the appendages of the perithecia, he gives (p. 65) the name *P. Berberidis* to the fungus on Berberis, as contrasted with *P. suffulta* on leaves of *Corylus Avellana*. No effort has been made to compare the material collected for this investigation with Palla's results for systematic purposes, but the writer can confirm most of Palla's observations on the intercellular hyphæ and haustoria. Palla finds that the haustoria on the intercellular hyphæ are found in the mesophyll cells in the two hosts he examined. As shown from a study of several hosts, Corylus,

[6] It seems worthy of mention that, on mature perithecia, the appendages in this genus do not extend parallel to the surface of the leaf, as in the young stages, but obliquely downward. The result is that the perithecia are raised into the air for the length of the appendages. The perithecia, therefore, fall off easily when the leaves are handled. It may be that the appendages serve the fungus as organs of distribution.

[7] Investigators who have thought of the Erysipheæ as purely epiphytic parasites, or as receiving their nutriment entirely from the epidermal cells, have been cited on p. 172. See also **27, 29, 31.**

Fraxinus, Cratægus, and Kornus, haustoria pierce the cells of the loose parenchyma in a minority of cases. Usually the intercellular hyphæ first penetrate the leaf to a region intimately associated with the fibro-vascular bundles (*fig. 31*) before producing absorbing organs. Sometimes haustoria are found in the cells between the bundles and the palisade cells, and sometimes in the palisade cells themselves. Palla observed hyphæ passing into the palisade layer, but he did not find haustoria there. In Xanthoxylum, however, haustoria frequently penetrate the cells of the loose parenchyma (*fig. 27.*) *Fig. 32* shows that the intercellular hyphæ which enter the stomata are either side branches of exterior hyphæ or the ends of original hyphæ. Except when the interior hyphæ arise as side branches immediately over the stomata, it is impossible to determine whether we have to do with an original germinating tube or not, so long as cross sections of leaves are used. If the stoma stands wide open, the initial cell of the penetrating hypha is not narrowed (*figs. 27, 28*), but upon the closing of the stoma the initial cell accommodates itself to the space left to it. It thus is narrow at the middle and becomes larger at the distal end (*figs. 30, 33*). Palla finds that the intercellular hyphæ of *P. suffulta* contain at most three cells (24, p. 7), and of *P. Berberidis* two (seldom three) more. The cells of the hyphæ within the leaves examined by me vary with the distance to be traveled before the production of an absorbing organ. Fewer than two cells were not found. The number is typically three to five. The distal cell of the intercellular hyphæ is sometimes extremely long. It is possible that, in tracing the sinuosities of the hyphæ through several sections, septa and nuclei may have been overlooked which would raise the number of cells to more than five. When the hyphæ produce their absorbing organs near the stomata, such hyphæ are noticeably larger than the surface hyphæ. But when the filaments extend a long distance through the intercellular spaces, some or all of the cells are more or less attenuated (particularly the distal cells.) An intercellular hypha may sometimes extend through more than a dozen sections. Haustoria do not appear

at the sides of the hyphæ exclusively, as Palla observed (**24**, p. 70), but frequently from the end, as in *figs. 29, 31*. In all of the hosts mentioned, excepting Xanthoxylum, the haustoria agree in structure with those of *E. communis*. *Fig. 31* shows the haustorium in one of the big parenchyma cells which form a sheath for the bundle. It also arises from the end of a hypha and contains a crystal which is so large as to distort the absorbing organ.

The haustoria of Phyllactinia on *Xanthoxylum Americanum* offer some striking differences in comparison with the ones just described. The intercellular hyphæ have thicker walls and the intercellular appressoria are conspicuous, flattened, sucker-like structures appressed tightly to the cells of the leaf (*fig. 28*). The leaves of Xanthoxylum have a thin layer of loose parenchyma. The bundles are near the lower epidermis. These facts of structure seem to influence the parasite. Its intercellular hyphæ, as a rule, are short and the cells are thick. They are more vigorous in appearance, the walls are less delicate, and they stain more readily than the surface hyphæ. Since the leaves of the host are thin the intercellular hyphæ are shorter than in those hosts where the haustoria are developed far from the stomata. No appressoria were observed on the surface hyphæ, though no special effort was made to find them. The appressoria of the intercellular hyphæ are numerous and conspicuous. Even beyond the point where the haustorium is produced, the hypha may adhere to the cell (*fig. 27*). The chief point of interest, however, is the absence of typical haustoria. In a long search through many sections I was unable to identify surely a single absorbing organ having the typical structure for haustoria of the Erysipheæ. There are numerous absorbing organs such as are represented by *figs. 27* and *29*. The penetrating tubes which pierce the host-cells are as minute as in Erysiphe, but the vesicles within the cells appear to have no protoplasmic contents. They have thick shining walls which, in exactly longitudinal sections, appear to be continuous with the walls of the host-cells. It was supposed at first that they were young haustoria differing

in the details of their development from the haustoria of Erysiphe; but their abundance and the many weeks for which the prickly-ash bush must have been infested when the material was gathered, make it evident that they are modified haustoria. It is to be seen that there is some resemblance between *figs. 27* and *29* and the early stages of penetration represented in *figs. 2* and *3* from Erysiphe. The haustoria of the fungus on Xanthoxylum certainly answer very well to the knob-shaped structures De Bary described, which were probably young haustoria. It is impossible to decide absolutely that they were, however, because of their similarity to *figs. 27* and *29*. Certainly if they represent dead haustoria, as De Bary thought, the vigorous mycelium must be nourished in some other way.

GENERAL CONSIDERATIONS.

The phenomena exhibited by the intercellular hyphæ of Phyllactinia are interesting in connection with what has been ascertained by several investigators in relation to the nutrition of fungi. It has been mentioned that the majority of the intercellular hyphæ in several of the hosts studied (excepting Xanthoxylum) take a more or less direct course to the regions near the bundles. The development by the fungus of the absorbing organs in regions abundantly supplied with available food, such as the parenchyma sheath of the bundles, indicates a selective chemotropism in the fungus. A selective chemotropism was reported by Miyoshi for several fungi in his paper already cited. Phyllactinia thus offers under normal conditions of growth a demonstration of the selective reaction which Miyoshi demonstrated by artificial means. This reaction enables Phyllactinia not only to surround itself with conditions which will insure it an uninterrupted supply of food and water such as is not insured to it while living as a purely epiphytic parasite, but also it is able to select within the leaf of the host those regions better supplied with food and water than the loose parenchyma. If the fungus is stimulated to place haustoria in cells joining the bundles to the palisade layer, or if haustoria enter the

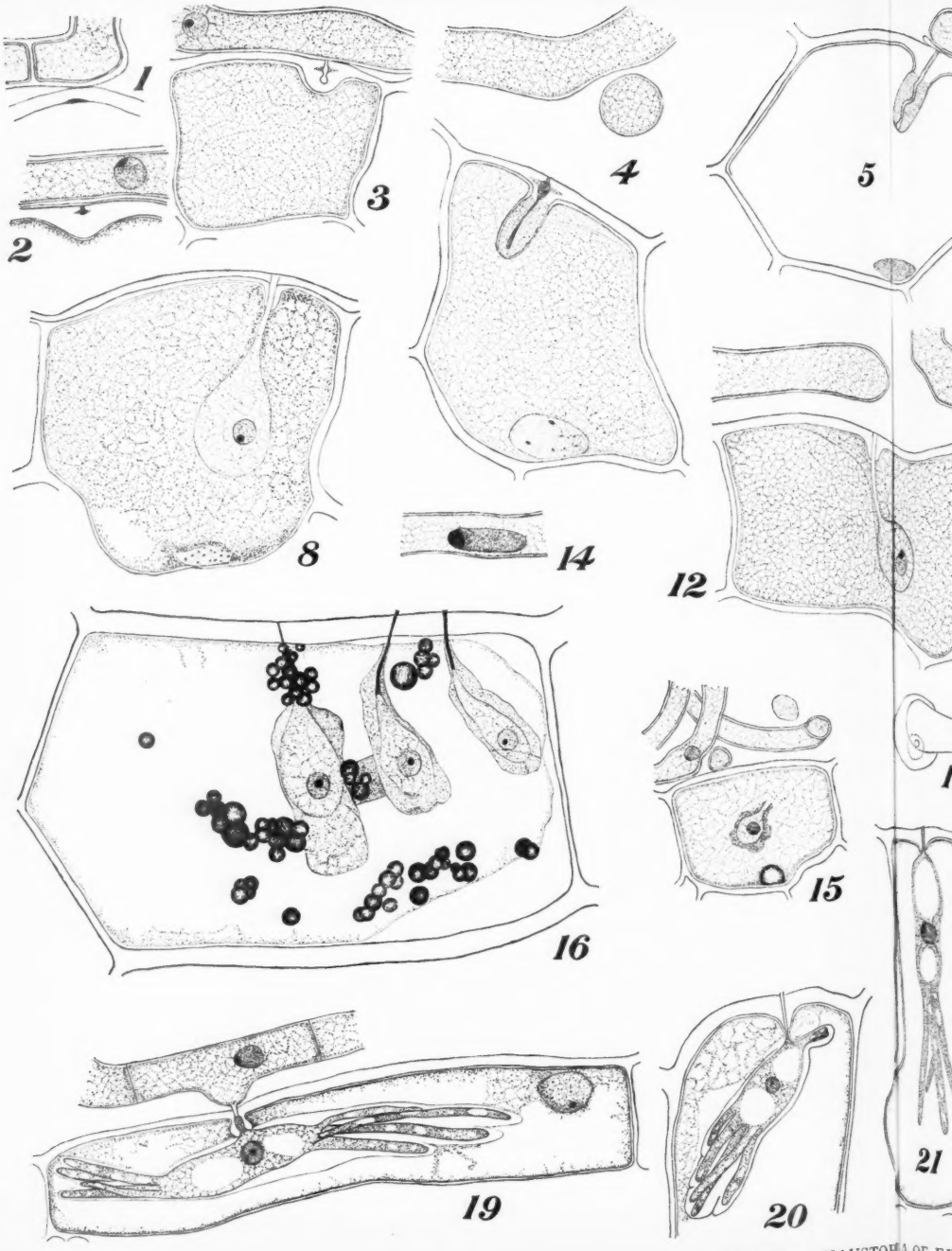
palisade cells, they are still at the very source of that supply of food by which the plant maintains its vigor and activity. The proportion of cases to be found in which the intercellular hyphæ do develop haustoria in these more favorable regions is larger than casual observation would lead one to think. By a study of the cells of the host-leaf in sections preceding and following the section which contains the haustorium, it may often be determined that the fungus actually has placed its absorbing organs in one of the favorable cells. It should not be thought, however, that this is done invariably. In Xanthoxylum the leaves are so constructed that the bundles are near the lower epidermis through the stomata of which the fungus finds access. All of the mesophyll cells, therefore, have a surplus of food. This fact would account for the number of mesophyll cells which contain haustoria.

If it be demonstrated that the mildew on Xanthoxylum does not possess typical haustoria under any conditions, it will be important to discover whether the apparently stunted haustoria can absorb food for the fungus as well as typical organs. If they are not effective, how far is the fungus nourished by saprophytic methods? In the first place, the intercellular spaces of the leaves of this particular host are abundantly supplied with organic material. On the part of the parasite itself it is noticeable that, when under the stomata, the intercellular hyphæ encounter parenchyma cells which block the way, the cells of the hyphæ are short, thick, and vigorous; not only when the haustoria are produced near, but also when the hyphæ have haustoria at some distance from the stomata. But the hyphæ which do not encounter such cells, but run a comparatively uninterrupted course before constructing haustoria, are more or less attenuated and are less vigorous in appearance. If some cell of the hypha in such a case lies in contact with a parenchyma cell (*fig. 33*, penultimate cell), that cell of the hypha is short, thick, and vigorous. Büsgen's results would seem to show that Erysiphe does not succeed as a saprophyte. At least, he found that its germinating tubes had a limited growth under the conditions

he was able to establish. He did not succeed in infecting pieces of leaves arranged for the purpose. If, under natural conditions of infection, the germinating tubes have a limited growth unless supplied with nutrient material from the host in some way, it is not clear how they can obtain it so as to grow down into the leaves for comparatively long distances, as Phyllactinia does, before producing haustoria, unless the fungus appropriates intercellular material. The subject is still open for investigation. It is possible, of course, that the first side branch, passing into the interior of the leaf, places an absorbing organ near the stoma and thus supports the whole branching system until other side branches in other stomata are able to assist.

There is some evidence to support the possibility of intercellular nutrition in this fungus, as has been established for others by Nordhausen, Ward, Büsgen, and Frank. This investigation, however, has not embraced the question of how far, if at all, the abundant intercellular material in Xanthoxylum leaves is available, though some facts were observed which suggest the possibility of intercellular nutrition of the parasite which have not been observed in other hosts infested by Phyllactinia.

There are two points connected with my observation of Erysiphe on the geranium leaf which may be mentioned briefly. At the end of a section where the scissors with which the pieces of leaves were cut had destroyed the section in part, a haustorium was found in what was clearly a subepidermal cell. Its connection with the surface was destroyed, but there is no doubt that it was a normal haustorium in one of these cells. Whether it was due to the chance presence of Phyllactinia on this host, whether Erysiphe occasionally adopts the practice of *Uncinula Salicis*, or whether it was Uncinula itself on this host, could not be determined. With this circumstance is related a note on page 9 of Ellis and Everhart's *Pyrenomycetes*. This note corrected the mistake of the artist (F. W. Anderson) who, it was supposed, wrongly represented (*fig. 3, pl. 1*) a germinating tube from a conidium of *Sphaerotheca Castagnei* as entering a stoma. My observations render it probable that the artist saw what he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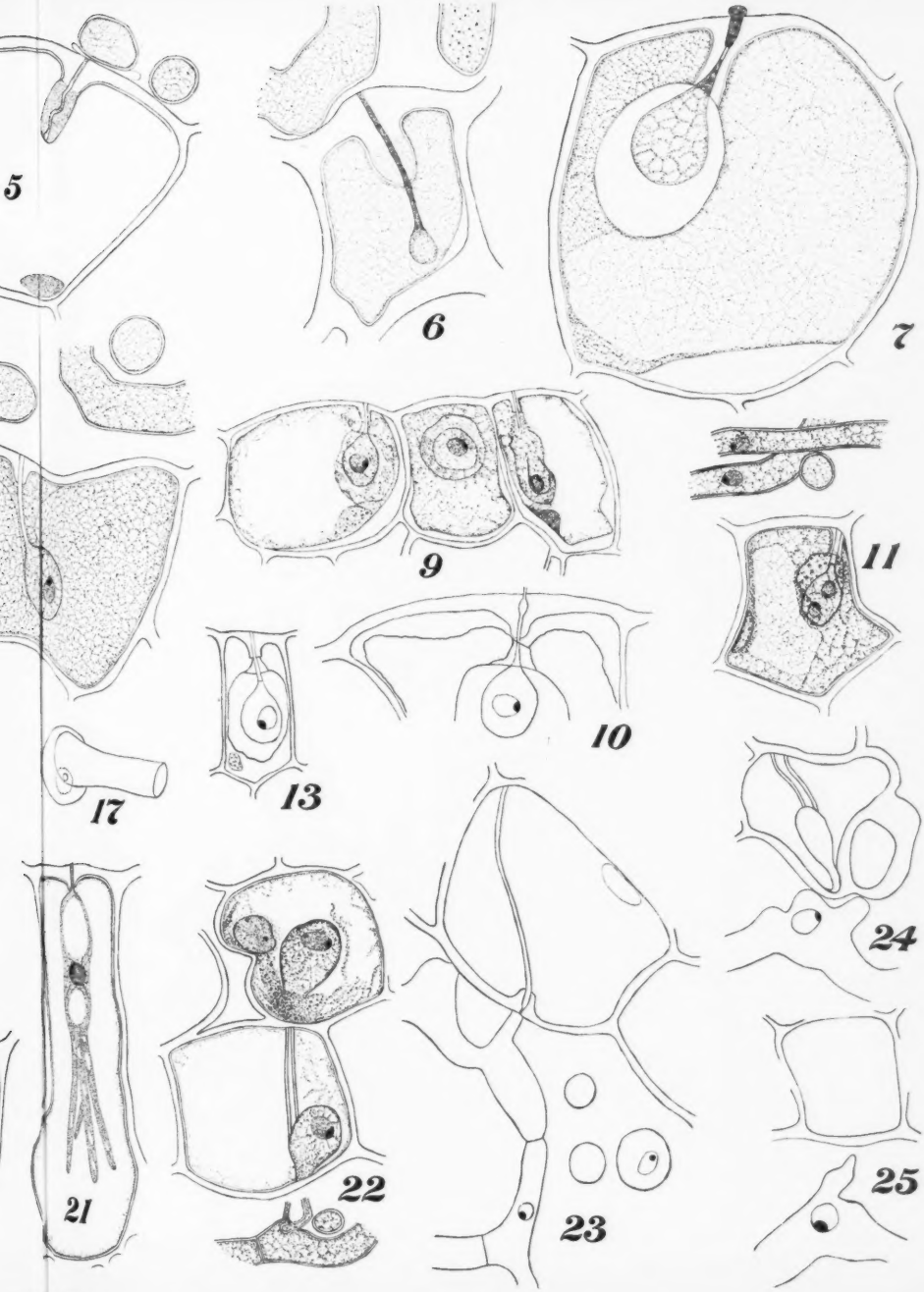
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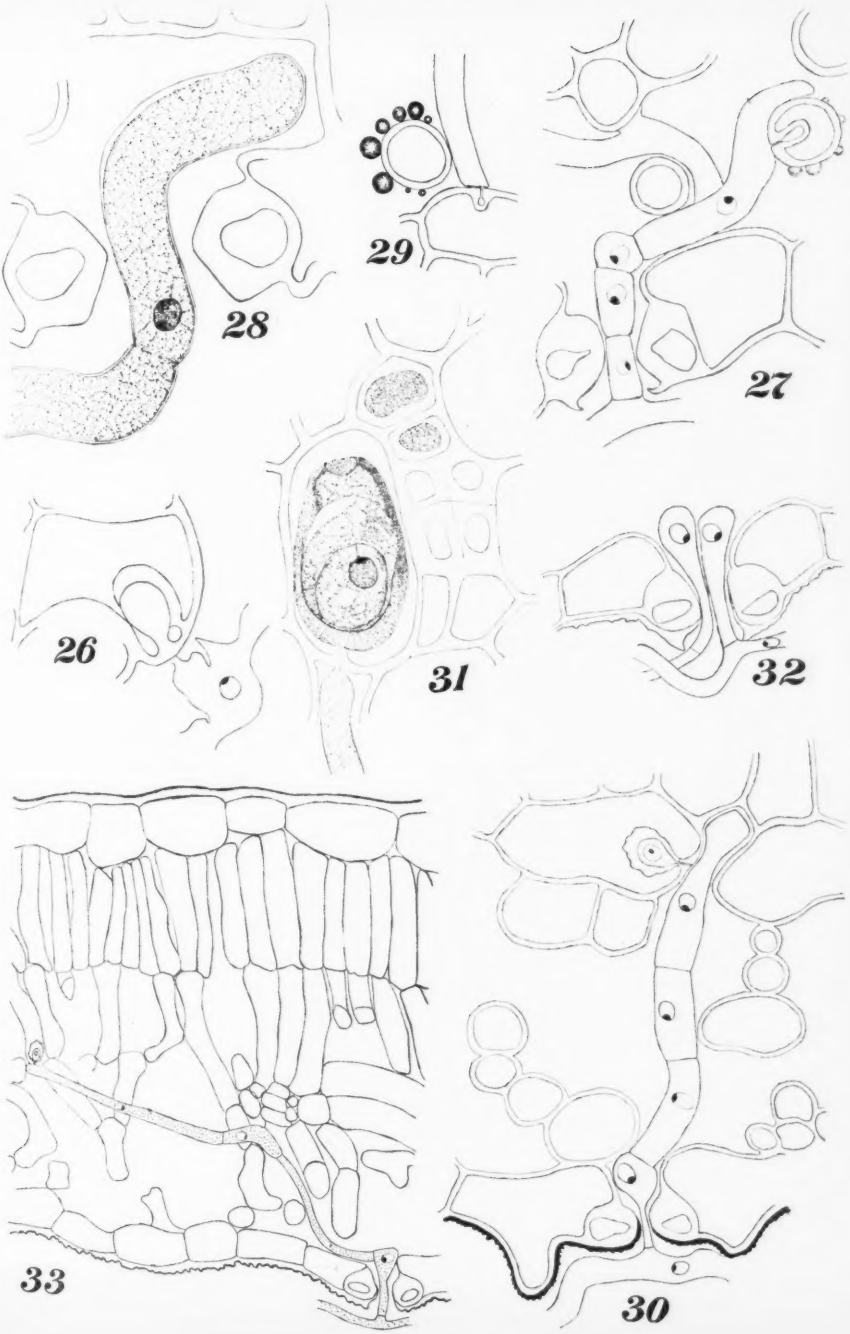

SMITH on HAUSTORIA OF ERYSIPHEÆ

represented, though it may have been a tube of Phyllactinia. Whether or not Sphærotheca has a similar habit to Uncinula, I have not determined.

It is a pleasure to acknowledge the assistance I have had in this investigation from Professor C. R. Barnes, under whom the work was begun, and from Professor R. A. Harper, under whom it was mainly accomplished.

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LIST OF GENERA AND SPECIES STUDIED.

Erysiphe communis (Wallr.) on *Geranium maculatum* L.
——— *graminis* DC. on *Poa pratensis* L.
——— *Galeopsidis* DC. on *Scutellaria lateriflora* L.
——— *Galeopsidis* DC. on *Galeopsis Tetrahit* L.
——— *communis* on *Polygonum aviculare* L.
——— *Cichoracearum* DC. on *Eupatorium perfoliatum* L.
Sphærotheca Castagnei Lév. on *Bidens cernua* L.
Podosphæra Oxycanthæ DC. on *Prunus* sp.
Microsphæra Russellii Clinton on *Oxalis corniculata stricta* Sav.
Uncinula Salicis DC. Wint. on *Salix discolor* Muhl.
——— *necator* Schw. on *Vitis* sp.?
——— *Clintonii* Peck, on *Tilia Americana* L.
Phyllactinia suffulta (Reb.)[1] on *Fraxinus pubescens* Lam.; *Cratægus punctata* Jacq.; *Xanthoxylum Americana* Mill; *Corylus Americanum* Walt; *Cornus stolonifera* Michx.

Such forms as are not discussed in the preceding pages have not been found to differ so materially from *Erysiphe communis* as to require a separate discussion of their haustoria.

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[1] The material has not been examined with reference to the classification of Phyllactinia proposed by Palla (**24**, p. 65).

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EXPLANATION OF PLATES XI AND XII.

All the figurés were drawn by the aid of the Abbé camera.

Magnification of *figs. 9, 11, 13, 22 to 30*, 900 diameters; *figs. 16, 28*, 2000 diameters; *figs. 32, 33*, 400 diameters; all other figures, 1800 diameters.

FIGS. 1–15. *Erysiphe communis* on *Geranium maculatum.*

FIG. 1. First stage in penetration, marked by spot on inner surface of host wall.

FIG. 2. Penetrating tube just beginning to make its way through epidermal wall. Wall thickens as tube grows.

FIG. 3. Having enlarged at a point in line with the inner boundary of the epidermal wall the tube continues its growth.

FIG. 4. Further stage in penetration. Cellulose papilla elongates as the tube grows. Distal end of cellulose in growth begins to show signs of disintegration. Nucleus of host-cell on basal wall of cell.

FIG. 5. Distal end of penetrating tube now begins to enlarge. Cellulose further disorganized. The proximal end of ingrowth not disintegrating, but destined to remain as collar about neck of haustorium.

FIG. 6. Young haustorium escapes from cellulose thickening and is developing without sheath.

FIG. 7. Stage before entrance of haustorium nucleus. Stretched and intruded plasmic membrane of host-cell forms bounding membrane of sheath, which in this case is devoid of contents.

FIG. 8. Haustorium without sheath.

FIG. 9. Middle haustorium in optical section, the two at end in longitudinal section. Sheath present about haustoria.

FIG. 10. Plasmolyzed cell showing collar as an ingrowth of cellulose from cell wall. Partly in perspective.

FIG. 11. Haustorium with two nuclei. Septum also found across neck.

FIG. 12. Haustorium without sheath. Protoplasm of host-cell adherent to sides of neck.

FIG. 13. Haustorium shows septum across neck.

FIG. 14. Elongated nucleus in mycelial hypha.

FIG. 15. Membrane absent from sheath, which here consists of lumps of disintegrated cellulose adhering to body of haustorium.

FIGS. 16–17. *Erysiphe Cichoracearum* on *Eupatorium perfoliatum.*

FIG. 16. Basal cell of hair containing haustoria.

FIG. 17. Shows unstained area about point of penetration. Remainder of host wall staining darkly.

FIGS. 19–21. *Erysiphe graminis* on Poa. Three branching haustoria.

FIGS. 22–26. *Uncinula Salicis* on *Salix discolor.*

FIG. 22. Epidermal cell containing one haustorium, while from the same appressorium another penetrating tube passes through the epidermal cell into the subepidermal cell. The sheaths are not visible.

FIGS. 23–26. Various forms of appressoria giving rise to two or more haustoria.

FIG. 27. Modified haustorium arising from appressorium and penetrating mesophyll cell. Host-cell shows exudations on its exterior. A second appressorium also shown.

FIG. 28–33. *Phyllactinia suffulta; figs. 28, 31* on *Fraxinus pubescens; fig. 30* on *Cornus* sp.; *figs. 27, 29, 32, 33* on *Xanthoxylum Americanum.*

FIG. 28. Part of an intercellular hypha. Guard cells drawn apart and hypha not compressed, as in *figs. 32, 33.*

FIG. 29. Smaller haustorium, and arising from end of hypha. Exudation on cell of leaf shown.

FIG. 30. Intercellular hypha consisting of four cells. Haustorium arising from side of distal cell. Host-cell below palisade cells.

FIG. 31. Haustorium arising from end of intercellular hypha and penetrating parenchyma cell connected with bundle. Haustorium contains a crystal.

FIG. 32. Stoma containing initial cells of two intercellular hyphæ, one a side branch. Origin of the other is indeterminate.

FIG. 33. Intercellular hypha, with haustorium in cell joining bundle to palisade cell. Middle cell of hypha is short and thick, and lies on cells of host.

STUDIES ON THE GEOTROPISM OF STEMS.

EDWIN BINGHAM COPELAND.

1. The absence of polarity in the hypocotyl of Cucurbita.

THE hypocotyl of Cucurbita, and, I suppose, of every plant whose cotyledons expand and act as leaves, is negatively geotropic in its ultimate reaction. When the hypocotyl is in any other position than the vertical, the under half of it grows more rapidly than the upper. This is regarded as a response to the unusual disposition of the burden of the parts of the hypocotyl, as they rest upon one another; and the seat of perceptivity and response is more specifically located in the green cortex.[1] The purpose of the reaction is to get the cotyledons into the light, which, when the seed germinates in the ground, will be accomplished by pushing them upward. Now it is evident without argument that an excess of growth of the under half of the hypocotyl will place its upper end in a vertical position, so that its further growth will be upward only in case the basal end is fixed in its position and the naturally upper end is free—a condition which is fulfilled in nature by a considerable growth of the root before the elongation of the shoot commences.

Teleologically, perhaps phylogenetically, the geotropism of the shoot has been developed along lines of "lengthwise" propriety: *i. e.*, in order to secure a particular linear arrangement of root, hypocotyl, cotyledon, etc. But in the individual plant today, according to Czapek's explanation (*loc. cit.*), which is the only rational one I am acquainted with, the response is to a disturbance of the normal "crosswise" arrangement, so that each growing part of the hypocotyl acts without reference to the parts more or less remote from the cotyledons.

The question as to whether or not any trace of the development of geotropism remains in its manifestation in the present

[1] CZAPEK, F.: Weitere Beiträge zur Kenntniss geotropischen Reizbewegungen. Jahrb. f. wiss. Bot. **32**: 248. 1898.

plant has seemed to me worthy an experimental answer. Such a trace would appear as a sort of polarity, such that if the fixed point of the hypocotyl were moved upward from the base, only the upper free part would remain disposed to become erect. To answer this question I transferred the fixed point at once from base to apex, in each case leaving the other end free. The result was unequivocal, and as the data from several experiments were in all essentials alike, it will suffice if a single series is reported.

The seeds were germinated on a net over water and the seedlings selected were perfectly straight and as uniform as possible. The hypocotyls, 6–6.5^{cm} long, were marked off into zones of 1^{cm} each, and these zones were numbered from the cotyledons downward. The end to be fixed was imbedded in a block of gypsum plaster, and these blocks were placed, with the hypocotyl horizontal, in a closed glass vessel containing some water. The experiment was begun at 10 A.M., April 12, 1899, and at 4 P.M. the free ends were all directed upward at angles of 50–70°, those having free cotyledons being somewhat more sharply elevated than those having free roots. They were left undisturbed for six days, at a lower temperature than Cucurbita likes, about 18° C. in general, and were then removed and the growth and curvature measured. The curvature is expressed in the following table in figures representing the radius of the arc, measured by a Sachs' cyclometer. Plants 2 and 4 had the roots imbedded; plants 1 and 3 the cotyledons, so that zone I was next the plaster.

PLANT 1.

Hypocotyl straight and erect (the roots in air) to within 6^{mm} of the cotyledons. The radius of the curve for the upper 5^{mm} of the hypocotyl and the exposed 5^{mm} of the cotyledons was about 1^{cm}.

Zone	I	II	III	IV	V	VI
PLANT 2.						
Curvature (in cm.)	15	9	6	3	5	15
Growth (in mm.)	3	3.5	2.7	2		
PLANT 3.						
Curvature (in cm.)	2	3	4	7	12	
Growth (in mm.)	1.7	1.2	1.3	1		
PLANT 4.						
Curvature (in cm.)	14	10	4	3	4	8
Growth (in mm.)	1.5	2	1.7	1	1	1

The conclusion, which has been anticipated, is that the response to gravity of the horizontal hypocotyl is always the same, whether the result is beneficial or, under artificial conditions, detrimental. It is a response to local conditions in each individual zone of the hypocotyl, and is executed without the slightest regard to the *relative* positions of the different zones, or the serial parts of the plant, roots, hypocotyl, cotyledons.

The pumpkin has even, figuratively, no brains. Its response to a stimulus is blind, like the instincts of animals: merely an effect, devoid in any individual instance of a purpose. As is often at least true of instinct, the response is not directly to the condition it is designed to correct, or to suit, but to something correlative, or merely concomitant. In response to a shifting of the pressure upon one another of the transverse elements of a tissue, the plant executes a change in its growth, which becomes of some service only when it results in a certain longitudinal arrangement of the plant-members; this longitudinal arrangement is the thing at fault, but the plant cannot perceive it. In nature the response meets the hidden purpose, but under changed conditions the same response is made, and is fatal. Certain flies flock at the scent of carrion, not in reality to gratify their peculiar æsthetic sense, nor yet to get a meal, but because it takes them where their eggs will thrive; the Dictyophora panders to their instincts; the carrion flies revel in its slime, and, mistaking the attribute for the reality, deposit their eggs where they rot. The behavior of the pumpkin and the fly is essentially the same; both react blindly, but in nature, fortunately.

A careful inspection of the table given above will show, in the different location of the region of greatest curvature in the plants with encased roots and in those with encased cotyledons, a nice demonstration that each zone of the hypocotyl can act for itself. In the former the hypocotyl is somewhat curved throughout, even in the most mature basal part, and most so about 4^{cm} below the cotyledons, the upper, youngest part being almost straight; while when the cotyledons were encased the curvature

is most marked within 1^{cm} of them, and the older part is straight. This difference could not occur if each zone were not able both to be geotropically irritated, and to respond to the irritation. If the experiments lasted several days it was found that the stems which were fixed at the apex were usually more curved than those fixed normally, at the base, so that in this case the end in the air was carried well beyond the vertical position. This was obviously because the youngest part remained horizontal, and as the older part matured with more or less curve the part still growing kept bending itself upright, and so carried the older part beyond the vertical.

The hypocotyls of *Helianthus annuus* and *Lupinus albus* and the epicotyls of *Pisum sativum* and *Phaseolus vulgaris* were tested, but showed no behavior different from that of Cucurbita, so that it is not worth while to encumber this paper with the individual results. The nutation of Phaseolus caused some queer curves, and the same would probably be found the case with Cucurbita when the epicotyl changes from orthotropic to plagiotropic. The behavior in response to stimulation by light is analogous. No experiments were undertaken especially to show this; but when seeds of Lupinus were germinated in holes in a floating cork in a glass vessel, and grew so that the cotyledons kept their place while the hypocotyls extended downward into the water, the latter became concave on the light side, and the roots were carried toward the window.

Any indication of real polarity is likewise wanting in roots. This is not easily demonstrated, as the curvature is largely executed in the roots of the plants I have been using, within 1.5–2^{mm} of the tip, and it is difficult to imbed them so that the tip will stay fast without encasing the part which should be free to react. Nevertheless, I have succeeded occasionally with the roots of Cucurbita, Lupinus, Helianthus, and Pisum, and in every case the result was an excess of growth of the upper side of the root, by which the shoot end of the plant was carried downward. This went as far as about 90°, but I have hitherto been unable to make the tip stay imbedded while the free end is bent

around indefinitely, as F. Darwin[2] did with the cotyledons of Sorghum.

2. The geotropism of split stems.

While it is certain that every growing part of the stem can perceive the geotropic stimulus and execute the response *in loco* it is not impossible that if the local perceptivity could be interfered with, a growing zone might respond to a stimulus transmitted to it from another part of the plant. My first experiments with split hypocotyls were with a view to answering the question; but they were not appropriate, because, as Sachs[3] showed, and as anybody can easily demonstrate, a half stem is in itself irritable. The results which they did yield, however, were surprising enough.

Cucurbita.—The first experiments were on Cucurbita hypocotyls, partly or wholly split, the split being either transverse or parallel to the plane of the cotyledons. Of three similar experiments it will suffice to report the following one, which began May 24, and lasted forty-eight hours. The growth is reported, and the angle made by the free end with its original horizontal position.

	Growth in mm	Curvature in degrees		Growth in mm	Curvature in degrees
1 Free	40	80	5 Split horizontal	18	180
2 Split vertical	8	75	6 Split horizontal	10	165
3 Split vertical	4	70	7 Split horizontal	5	180
4 Split horizontal	13	110			

No. 1 was fastened in place without imbedding; nos. 5 and 6 had the cotyledons imbedded; and the others, the roots. The

[2] F. DARWIN, in "Botany at the British Association," Nature **61**: 67. Nov. 16. 1899. After other evidence that geotropic perceptivity is localized in the cotyledon while the hypocotyl executes the response, he says: "If the seedling is supported by its cotyledon (which is fixed in a horizontal position) while the hypocotyl projects freely . . . . the hypocotyl begins to curve upward . . . and it does not cease to curve when the free end points vertically upward; the curvature continues indefinitely, so that the hypocotyl curls into a spiral of three or four rings."

[3] SACHS: Ueber Wachsthum und Geotropismus aufrechter Stengel. Gesammelte Abhandlungen **2**: 969. 1893. In the experiment Sachs reports, the growth of the lower half did not overcome the tissue tensions.

depressed growth of nos. 2 and 7 is correlative with the imbedding, as well as due to the wound. Removing the plumule does not hinder the elongation of the hypocotyl. When the split was horizontal the halves became bowed apart, and the angle of curvature given is the least at which they could be brought into continuous contact.

The first notion suggested by the excessive curvature of the hypocotyls with horizontal split surface is that they are responding to a stimulus received by the imbedded part of the plant. But the facts that a half stem is known to be in itself irritable, and that the extreme curvature, 180°, occurred whether it was root or cotyledon that remained horizontal, point toward the conclusion that in the experiment each half of the split hypocotyl responds only to a stimulus received *in loco*; and that a half hypocotyl has something in its own structure, independent of any comparison of conditions with the other half, which will make it grow more rapidly if the split is the upper than if it is the lower surface.

Two plants were next split from the tops well into the roots, one having the cotyledons split, the other separated; both had the roots imbedded. The halves of one were too weak to become quite erect, but those of the other bent up side by side, and after they became erect the lower half slid along the upper so as to reach beyond it. In both cases the growth of the lower half exceeded that of the upper by 3^{mm}. The experiment was repeated, giving a little less difference.

July 13, a number of plants were split from end to end, and the entirely separated halves imbedded side by side, some with the roots, others with the cotyledons free, all with the cut surface horizontal. The growth in forty-eight hours follows:

	Growth of upper half in mm	Growth of lower half in mm
1.	2.5	3.5
2.	2.0	3.5
3.	2.5	4.0
4.	3.5	5.0
5.	2.0	2.3
6.	3.0	4.0

In every instance the lower half grew more than the upper.

July 14 the experiment was repeated with older plants. The average growth of nine plants in forty-eight hours was: in the upper half, 1.5^{mm}; in the lower half, 2.2^{mm}. In every instance except one the greater growth was made by the lower half. It occasionally chanced that one half twisted into the other's position, which caused the difference to be wanting or less marked.

Later in the year in connection with work on other plants, I put five split plants into glass tubes too small to let them bend. The average growth of the lower halves in three days was 26^{mm}; of the upper halves, 16^{mm}. At the same time I made a small attempt to see what is the rate of growth of a horizontal half stem in either position as compared to one in its natural erect position. Three plants were split throughout, and one half of each was put into an upright glass tube. In three days the average growth was 4.8^{mm}. The other halves were put into horizontal tubes, with their split surfaces up, and grew in the same time on an average 14.3^{mm}. Of three other plants the average growth of the erect halves was 24^{mm}, and of the horizontal halves with split surface down, 24.3^{mm}; but two of these latter had twisted so that part of their growth was made with the cut surface up. The comparative growth of erect and horizontal halves was more fully experimented on with Lupinus.

Phaseolus vulgaris. Three epicotyls, 4–5^{mm} in length, were split November 3, and the cotyledons were imbedded so that the split surfaces were horizontal. In three days the average growth of the upper halves was 3.2^{mm}; of the lower, 5.7^{mm}. The curves necessary to bring the halves together were 95–145°. November 20, six epicotyls were split, and the halves fastened in the same positions with glass needles. In two days the average growth of the upper halves was 25^{mm}; of the lower, 27.2^{mm}. Small as the average difference is, the lower half was longer in every instance.

Caladium sp. On large corms that had been brought into the greenhouse for the winter the stubs of the shoots were still growing slowly. These stubs were made up of some very young

leaves in the middle, surrounded by the fleshy petioles of the leaves the rest of which had been removed. Two of these petiole stubs were present, each reaching around far enough so that its edges lapped over one another. These petioles should execute any curving that occurs. I cut the end of the stub off square, and then split it into several slices, in such a plane that the upper and lower parts of the larger outer cotyledon were symmetrical, and placed the corms so that the split surfaces were horizontal. The atmosphere was unfortunately not saturated, and cutting and splitting the fleshy parenchyma gave such an opportunity for evaporation that in most cases after a week a shortening instead of an elongation had occurred. Nevertheless, a slight upward curve of each slice was noticeable, and a difference in their growth could be detected in spite of the shrinking. The following two experiments may represent the five made:

1. Diameter of stub, 3mm. Cut into four equally thick slices. Change in length of outer petiole in six days:

1st (undermost) slice.		no change
2d	"	—1 mm
3d	"	—1.3mm
4th	"	—2 mm

2. Diameter 35mm: in five slices. Change in six days:

1st (undermost) slice.		+1 mm
2d	"	—0.4mm
3d	"	—0.6mm
4th	"	—1.0mm
5th	"	—2.0mm

It appears then that where these composite stem structures are split into a series of slices the growth of these is successively less from below upward. Some of these slices consisted (aside from the epidermis) entirely of the large celled cortical parenchyma, and seemed able individually to execute geotropic curvatures. Caladium is the only subject with which I have succeeded in getting a series of longitudinal slices of sufficiently equal thickness to give any kind of results.

Helianthus. Nine hypocotyls of the "mammoth Russian" variety were split, the cotyledons being either separated or split, and the split extending 1cm into the root. They were placed in horizontal glass tubes. After a day, four plants in which the difference in the growth of the halves was well marked were turned over, so that the halves exchanged places.

	December 5. Length in mm.	December 6. Growth in mm.		December 8—Growth from December 5. in mm.	
		Lower half.	Upper half.	Former lower half.	Former upper half.
1.	17	6	3	8	6
2.	30	8	5	15	26
3.	27	8	6	13	26
4.	25	8	4	16	15
5.	26	8.5	5		
6.	13	9	8		
7.	26	6	5		
8.	15	6	5		
9.	35	18	16		

The average growth of the under halves of the first four during the first day was 7.5 mm: during the following two days, when they were the upper halves, their average was only 5.5 mm. The average of the upper halves changed at the same time from 4.5 mm to 13.75 mm. There is no possibility of error either from unequal splitting or individual variability in these results.

Lupinus albus. The large, straight, solid hypocotyls of Lupinus are the finest subjects I have found for these experiments, and have been very freely used. November 15 four plants were split throughout, and imbedded at either end. After three days the average growth of the upper halves was 4.25 mm; of the lower halves, 10.5 mm. The lower half was always the more curved, in spite of the tissue tensions which at first bent it downward. It was indifferent whether the cotyledons were split or separated. Of a number of plants started November 17, and marked into 1 cm zones, the following two were interesting in their behavior. Both twisted so that the halves changed positions. After three days the growth of each half of one of them was 14 mm: at first the lower half gained (as was shown by measuring the individual zones), and then after their positions were reversed the other caught up. The upper and lower halves of the other plant grew respectively 15 mm and 13 mm, but before they changed places the lower was 2 mm ahead. Of six plants split and put into glass tubes, November 28, so that they might grow in length but could not curve, the average excess in length of the lower half after two days was 5 mm. Of seven plants

treated in the same way December 1, the average growth of the upper half in two days was 4.4^{mm}; of the lower, 9.1^{mm}. Of thirteen plants split 1^{cm} into the root and placed in horizontal tubing, the average growth of the upper halves in two days was 2.4^{mm}, and of the lower halves, 4.4^{mm}. Three plants were turned over; and after two more days the halves of two of them were equal, but in the other the difference had increased.

It has now been shown for hypocotyls and epicotyls, hollow and solid stems, fixed at either end by imbedding in gypsum plaster or pinning with glass pins, or grown in glass tubes, that the rate of growth of an isolated half stem is greater, in general perhaps twice as great, if it occupies the position of the inferior half of an uninjured prostrate stem, than if it is in the position of the superior half. As to the fact, the proof is surely sufficient. But so far no explanation has suggested itself, which was not more easily confuted than conceived.

After looking in vain for a real reason, I turned to the mechanism of the growth, but have been unable in a considerable number of experiments to detect any well marked or constant difference in turgor between the halves. If the turgor of the growing region at a fixed distance below the insertion of the cotyledons is determined it will be found less in the upper half, but this is because the growing region is shortened. If the zone which is elongating most rapidly is tested in each case (this will be perhaps 2^{mm} nearer the base in the under half) there will be found almost no difference in the turgor. The results from testing a number of plants were very constant, and the following may serve as an example. The halves had been horizontal for four days. Turgor is measured in percentage concentration of KNO_3 necessary to begin plasmolysis.

Lupinus albus.

Growth		Upper half 7^{mm}		Lower half 15^{mm}	
		Growing part	Grown part	Growing part	Grown part
Turgor	Pith	4	3	4	3.5
	Cortex	4	3–3.5	4	3–3.5

Ceteris paribus, however, the more rapid growth of the lower half would depress its turgor,[4] so that the equality observed indicates that with equal growth the lower half would have its turgor raised. It was noticeable that in general the relation of turgor in pith and cortex was the same in both halves (as in the growing part, in the figures just given); although to bring a pressure to bear against the tube which kept them straight, one half should manifest an excess of turgor in the cortex, the other rather in the pith. I do not know whether or not the entire stems would show any difference in the turgor of the halves, such as Pfeffer[5] observed in some grass nodes; but they do exert an upward pressure by the elimination by growth of the tension between the walls and cell-sap of the under side, so that the osmotic pressure is available for outside work. If a hypocotyl of Lupinus be removed from a horizontal glass tube and immediately split, the lower half stretches out, often at least 2^{mm} longer than the upper, and this difference is maintained after entire plasmolysis.

To determine the effect of the position of the horizontal half-stems on the rate of growth, as compared with the normal upright position, I paired a number of plants, split them, matched the halves of each plant with those of the other plant of the same pair, put them into glass tubes, and placed one tube erect, the other horizontal. Then one half of *A* and one half of *B* were erect; the other half of *A* was horizontal with the split surface up, and the other half of *B* was horizontal with the split surface down. They were wrapped in moist filter paper, and except for their position with regard to gravity were under as like conditions as could be desired. Of a series of six plants treated in this way, the growth of the erect halves in two days averaged 7^{mm}. The growth of the horizontal halves, whose cut surface was downward averaged 6.8^{mm}. At the same time the complementary six plants averaged: the erect halves, 8.1^{mm}, and the horizontal halves, with split surface up, 17.1^{mm}. Dec. 8, ten

[4] COPELAND: Ueber den Einfluss von Licht und Temperatur auf den Turgor. Inaug.-Diss. Halle a. S. 1896.

[5] PFEFFER: Druck und Arbeitsleistung durch wachsende Pflanzen.

pairs of plants were treated in the same manner. In three days the average growth was:

Of ten erect halves	15.7^{mm}
Of corresponding horizontal halves, split surface down	13.9^{mm}
Of other ten erect halves	12.8^{mm}
Of horizontal halves, split surface up	22.9^{mm}

Or, calling the growth of the erect halves 100, that of the horizontal halves with split down was 88.5; that of horizontal halves with split up, 178.9.

The growth of the isolated under half then is decidedly accelerated, while that of the upper half is in a lesser measure retarded. Sachs[6] long ago showed that this happens when an entire stem executes its response to geotropism, and it is interesting to note that isolation of the halves does not affect the quality of the reaction at all. This ought to give the quietus to all of the various theories which would explain the execution of the geotropic response by processes taking place entirely in either half.

The behavior of split stems emphasizes the fact that geotropic irritability is dependent upon the relative positions of the tissues of the stem: and seems to me to point toward a more intimate connection of the perception of the stimulus with the execution of the response than we have hitherto felt justified in assuming. The execution of the response by whole stems does not demonstrate any transverse transmission of a stimulus by which the halves compare their positions, for the behavior of the separate halves shows that no comparison is required.

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[6] SACHS: Längenwachsthum der Ober- und Unterseite horizontal gelegter sich aufwärts krummender Sprosse. Gesammelte Abhandlungen **2**: 945. (From Arb. des botan. Inst. zu Würzburg **1**: 193. 1872). On p. 955 he says: "Bei der Aufwärtskrümmung eines frei horizontal gelegten Sprosses wächst von je zwei gleichnamigen Gewebestreifen immer der der unteren, konvexen Seite stärkes, der der oberen, konkaven Seite schwächer als die gleichnamigen Gewebestreifen eines aufrechten Sprosses in derselben Zeit."

BRIEFER ARTICLES.

THE NUTATION OF HELIANTHUS.[1]

In a former contribution[2] the writer presented the results of extended observations on the nutation of the wild variety of *Helianthus annuus*. Considerable subsequent study in the same direction has fully confirmed the statements made at that time. It was, however, impossible to present satisfactory illustrations of the plants in the field, no camera being at hand when the observations were made. Since there seems to be some skepticism as to the fact of nutation, it was thought desirable to add a few more recent studies and some photographs showing the actual appearance of the plants in the field.

FIG. 1.—Cultivated *Helianthus annuus* at 6 P.M., three plants showing the westward nutation, and two with the heads tipped to the east.

During the summer of 1898 a series of observations was made in Columbus, O., on the common cultivated variety. The cultivated sunflower behaves very much like the wild one, except perhaps that it appears somewhat less striking in its reactions. The growing plants nutate from 60° to 90° west in the evening (*figs. 1, 2*), and from 50° to 70° or more, east in the morning (*fig. 3*). At night the leaves droop and the tips point downward.

When anthesis begins nutation ceases and the heads are tilted toward the east or northeast (*fig. 4*). Not only the main terminal heads but also some of those on the side branches take this position.

[1] Contributions from the Botanical Laboratory, Ohio State University. VII.

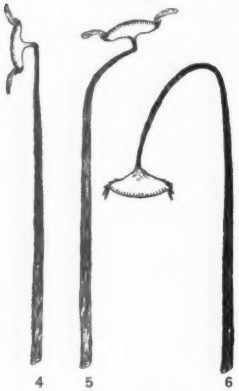
[2] Observations on the nutation of Helianthus annuus. BOT. GAZ. 25: 395–403.

The effect is most striking, however, in the case of plants with a single large head. It was observed that plants growing on the south

FIG. 2.—Cultivated *H. annuus* just before sunset, showing westward nutation.

FIG. 3.—The same plant as in *fig. 2*, at 7 A.M. the next morning, showing eastward notation.

side of a house did not tip to the east but to the south. This may have been caused by the reflection of the sunlight from the wall. The eastward position is often disturbed by the wind, so that the heads may appear to face in any direction. Sometimes the heads tip to the east while the stem below still continues to nutate (*figs. 4, 5*). This condition gave a very unique appearance to the plant when nutating in the evening. The same phenomenon has since been observed also in wild *Helianthus annuus*. After the seeds begin to develop the weight of the head bends the stem over, and the sharp angle caused by the tipping disappears (*fig. 6*). *Fig. 1*, taken at six o'clock in the afternoon, shows well the mode of nutation and also the eastward tipping of some of the flowering heads. The tipping of the head is of advantage in bringing the bracts of the involucre



FIGS. 4, 5, and 6.—Diagrams showing tipping of heads at anthesis (4, 5), and position when fruiting (6).

into the best position for photosynthesis, and appears to be a definite physiological adaptation. The downward turning of the head which occurs later may be produced by the weight of the developing seeds, but it must not be forgotten that this is also a decided advantage. The whole large disk filled with seed is thus well protected from the rain, the dying bracts, no longer useful for food manufacture, forming a roof which sheds water very successfully. This position also permits

FIG. 7.—Wild *H. annuus*, 7 A.M. July 17, 1899, showing eastward nutation.

FIG. 8.—The same group of plants as in *fig.* 7, at 7 P.M. of the same day, showing the more prominent westward nutation.

the seed to fall readily to the ground and at the same time affords considerable protection from birds, many of which are very fond of the seed.

During the summer of 1899 some observations were again made upon the wild variety of *H. annuus*, in Clay county, Kansas. There is nothing new to add to the report in my former paper, but a number of photographs are presented showing the character of the nutation. *Fig.* 7 shows a group of plants at seven o'clock in the morning of July 17, and *fig.* 8 represents the same group at seven o'clock of the evening of the same day. The more pronounced nutation in the evening is very apparent. *Fig.* 9 shows a field of young sunflowers just at sunset on June 27. The plants in the foreground show the striking

effect of a large field of plants all bending to the west. The tipping of the heads to the east or northeast is at times very prominent. *Fig. 10* shows a small patch of plants with the heads in this position.

FIG. 9.—A field of wild *H. annuus*, just at sunset, June 27, showing the pronounced westward nutation in young plants.

The writer knows of no better plant for the study of the light relation of leaves than *Helianthus annuus*, and it can be made an object of great interest to the young student.

Some observations were also made upon *H. petiolaris*. It was observed to nutate 90° west in the evening, before the heads came into

FIG. 10.—A patch of wild *H. annuus* at noon, August 23; the heads tip toward the northeast.

bloom, the nutation being nearly as marked as in *H. annuus*. On opening, the heads generally tip and the direction is usually to the northeast, at least for the terminal ones. But this movement is much less prominent than in *H. annuus*.—JOHN H. SCHAFFNER, *Columbus, Ohio*.

PTERIS CRETICA IN ILLINOIS.

THE CRETAN brake is a familiar plant in our dwelling houses and conservatories. It is said to be a native of Florida, Mexico, Guatemala, Italy, Corsica, Abyssinia, from the Ural mountains to Arabia, Himalayas, Philippines, Japan, and the Hawaiian islands.

In Mt. Carmel, Ill., it has long been one of the most common pot plants in our homes. About five years ago I first found it growing in my well, where it has continued to thrive ever since. Below about three feet from the surface it remains green throughout the year, and is now (February 15, 1900) thrifty and in all stages of development from mature fruiting specimens down to small plantlets.

Last summer I found it in a second well; and today it was shown me in a third. In each instance I learn that the plant has been cultivated in the adjoining house, whence the spores have probably found their way to the wells.

So I think it would be proper to add this beautiful fern to the introduced flora of Illinois, with this peculiar habit at the north.—J. SCHNECK, *Mt. Carmel, Ill.*

OPEN LETTERS.

THE RESEARCH STATION OF THE ROYAL BOTANIC GARDENS OF CEYLON.

I SHOULD like in a few words to call the attention of American botanists to the new research station which is now almost completed in these gardens, and to the advantages which are offered here to botanists desiring to work in the tropics. A more detailed account of the establishment under my charge, with plan of the new laboratory, will be found in *Nature* of November 9, 1899.

The Royal Botanic Gardens of Ceylon form a department of the public service, dating from 1812. In 1821 the headquarters were established at Peradeniya, a suburb of Kandy, from the center of which town the garden is about four miles distant. There are several good hotels in Kandy, and the gardens can be reached by rail or road; a bicycle is perhaps the most convenient, and will be found very useful in traveling in the island, the roads being on the whole excellent. The garden lies in a very beautiful situation, in very mountainous country, at an elevation of 1550 feet above the sea. To this fortunate circumstance the garden owes the great advantage in the matter of climate and healthiness that it possesses over most other tropical stations. The nights here are always cool, and the neighborhood of Kandy is practically free of malarial fevers, so that with reasonable care no risk of health need be run in living here. The mean annual temperature is 76° F. The hottest months are March and April, with a mean temperature of 79°; the coolest January and June (74°). The laboratory and library are cool buildings, and in them during the last two years the extreme range of the thermometer has been between 65° and 82°. The annual rainfall is about ninety inches, fairly evenly distributed over the year; the wettest periods are in June and July and in November and December, at the beginnings of the southwest and northeast monsoons respectively. On the whole, the best time to visit Ceylon is from October to March; but once here the climate is much the same all the year round, the objection to coming from Europe in the summer being the heat in the Red Sea and the discomfort of returning to a cold climate in winter.

The area of the garden is 150 acres; it contains a splendid collection of tropical plants, and is arranged like an English park, with wide lawns. In the center lie the buildings of the museum, library, herbarium, and laboratory, close together. The museum is chiefly devoted to economic botany,

and contains a very good collection of local products. The library contains about two thousand books and papers, and is rapidly growing. About seventy periodicals are taken or received in exchange, and among them are included most of the important scientific botanical journals. The herbarium contains a Ceylon collection, a general tropical collection, and a collection of the plants growing in the gardens. The new laboratory for research lies to the north of the herbarium, and is a single-storied building 75 × 40 feet, including veranda on the west end. The length of the building runs east and west. On the north side are two rooms, one for general microscopic and morphological work, 36 × 18 feet, with four good working places, and one for physiological work, 18 × 18 feet, with two places. On the south side is a room for chemical work, 18 × 18 feet; a room for work in economic and pharmaceutical botany, 26 × 18 feet; and a small private laboratory, 18 × 10 feet. On the east end is a veranda, 8 feet wide, of which the two ends are built up so as to form a dark room and a lavatory, while the intermediate part forms a space 18 × 8 feet in which experimental work causing unpleasant smells or requiring open air can be carried on. The west veranda is partially closed in with a low trellis and wire netting to form a room for the breeding of insects, etc. The laboratory is fitted with the usual apparatus for work in botany, chemistry, and entomology. It contains altogether eleven good working places, of which five or six are usually occupied by the resident staff, leaving five or six available to workers from abroad, who will be heartily welcomed and given all reasonable facilities and assistance in prosecuting their researches.

The value to a botanist of a period spent in the tropics is inestimable, and there is no country more favorable than Ceylon for the study of every form of tropical vegetation within a limited area. Every variety of climate is found within the island, which has about six times the area of Jamaica, and can be easily reached by railway and coach, and there are good accommodations for travelers in almost every part of the colony. Branch gardens are kept up in four places in different climatic zones of the island. At Henaratgoda, on the main line of rail to Colombo, and eighteen miles from that town, there is a small garden of about forty acres, of which twelve are occupied by untouched jungle, the remainder being cultivated chiefly in economic plants; there is a small laboratory room in the garden and a resthouse about a mile away at the station. The climate here is very hot and steamy, the garden lying at thirty feet above the sea level. The rainfall is about 110 inches per year, distributed much as at Peradeniya, and the mean temperature is about 82° F.

A second branch garden is at Hakgala, at an elevation of 5600 feet. It occupies an extremely beautiful situation about six miles from the great sanitarium of Ceylon, Nuwara Eliya. The total area of the garden is 550 acres, of which 40 are cultivated, and contain a fine collection of European, American, Australian, and other temperate plants. The rest of the garden consists

of untouched jungle and savannah land, occupying the steep side of the Hakgala mountain to an elevation of 6800 feet. The vegetation of this high level region is very interesting; the flora contains a large proportion of European genera. The Horton Plains, where there is a resthouse at an elevation of 7200 feet, form a magnificent collecting ground for the botanist, and lie about eighteen miles from Hakgala. Nuwara Eliya, at an elevation of 6200 feet, contains good hotels, has a temperate climate (mean temperature 57°), and is surrounded by hills on which the natural vegetation remains untouched.

A third garden lies at Badulla, on the eastern side of the main mountain mass of the center of the island, at an elevation of 2200 feet. Here the climate is different from that at Peradeniya, in having the driest period at the end of the southwest instead of the northeast monsoon, so that the periodicity of the vegetation is different, and fruits which ripen at Peradeniya in April ripen at Badulla in August.

A fourth branch is at Anuradhapura, the famous "buried city" in the north of the island. Here there is an Indian climate and flora, the weather being dry during the greater part of the year, so that only xerophytic plants occur.

A visit to the branch gardens alone thus introduces the botanist to a great variety of climates and floras; but there are several other types of flora to be seen, *e. g.*, that of the coast, of the river estuaries, the mangroves, and so on: all are easily reached by rail or road. Ceylon is very easily reached, there being direct lines of steamers from Colombo to almost all parts of the world. Round the world tickets at a cost of $525 to $625, first class, can be obtained, which enable a visit to be paid to Europe, thence to Egypt and Ceylon, and home *via* Australia, or *via* Singapore, Hongkong, Japan, and Honolulu to San Francisco. Return tickets to Colombo from London are from $350 to $450 first class, $250 to $300 second class; the latter is very comfortable, especially on the French and German lines. No outfit is necessary beyond a supply of the clothes usually worn in summer; drill, khaki, and flannel clothes can be bought here more cheaply than in Europe. The cost of living in hotels and resthouses is from seven to nine rupees per day, and three rupees are equal to $1.

Information about Ceylon may be obtained in many books, of which the following may be specially mentioned: *Ceylon*, by Sir E. Tennant (now out of print); *Ceylon in 1893*, by J. Ferguson; "The flora of Ceylon as affected by climate," Trimen, *Journal of Botany*, 1886; *Flora of Ceylon*, Trimen, 1893–1899, 5 vols.; "Botanic gardens in the equatorial belt," Goodale, *American Journal of Science* **42**: 173. 1891.

Intending visitors should communicate with me some time in advance, mentioning the line of work they propose to take up, with any special facilities they may require, *e. g.*, the planting before their arrival of special

experimental beds, the provision of any unusual apparatus or materials, and so on.—JOHN C. WILLIS, *Director Royal Botanic Gardens, Peradeniya, Ceylon.*

PATTERN FLOWERS AND METAMORPHOSIS.

C. R. B., in reviewing my text-book on p. 69 of the January GAZETTE, asks:

> Why assure a student that "a flower will obey certain well-defined laws," when the bulk of the chapters on the flower are concerned with explaining how they "disobey" these "laws," and in defining terms that are used to describe departures from a purely imaginative pattern? The whole treatment of the flower, indeed, proceeds upon the pernicious theory of metamorphosis.

Since the question has been asked, I trust that you will allow me to answer it, and in my own way.

My critic's quotation falsifies me, in sense as well as in word, and this falsification furnishes the only basis for his question. The statement is: "The typical flower will obey certain well-defined laws of structure as regards the following characters:" It may be wrong, but it at least allows its author the defense of reason, which is denied him by the misquotation. That statement was written in the light of an individual acquaintance with hundreds of such typical flowers, which the critic says are "purely imaginary." Since there are scores of thousands which vary from the pattern, the proportion of pages devoted to classifying such variations was considered appropriate. Is it not proceeding *ex cathedra* to call the theory of metamorphosis "pernicious"? May we not be credited with at least a knowledge of the attempts which have been made to get away from it, and a personal conclusion that that course leaves us no working basis which does not fail at the first test? To me the reading of Engler and Prantl's *Pflanzenfamilien*, and the actual study of the great number of flowers which I have examined during the last ten years is more convincing than any of the speculative "thought" or unproved theories which have been brought forward.—H. H. RUSBY.

[Dr. Rusby is quite justified in claiming misquotation, and I sincerely regret having been guilty of giving a false impression of his meaning, through my own misapprehension of the chapter criticized. My impression was derived from the chapter heading:

LAWS OF FLORAL STRUCTURE AND THEIR (*sic*) DEVIATIONS,

and from the conspicuously printed "laws," thus:

> LAW 3: REGULARITY.— *The parts composing one circle are all of the same form and size.* A flower all of whose circles obey this law is regular. . . . .

Having examined these various laws and been impressed by their nullity, I was *not* impressed by the word *typical*, which occurs in two sentences of

the introductory paragraph only, though with general application throughout the chapter. I am blameworthy for this oversight; perhaps the author is not wholly blameless for the impression which led to it.

I also am stating a personal conclusion when I call the theory of metamorphosis pernicious. This conclusion is the basis of my criticism of the discussion of the flower. I call any theory or thinking pernicious which leads us to hold and to state a subjective conception as an objective reality. The fundamental postulate of the theory or metamorphosis is wholly conceptual in that it assumes a type or pattern for a member, such as a leaf, or group of members, such as a flower. The following, from p. 34, illustrates this and might have been written by Goethe himself]:

> Progressive metamorphosis also occurs. It is seen in the gradual transformation of bracts, themselves transformed leaves, into sepals in the barberry (fig. 61), and of sepals into petals and of petals into stamens (fig. 62) in the water lily. Even stamens may become metamorphosed into carpels and carpels into stamens, one instance being the flowers of the willow, where organs have been seen intermediate in appearance between the two.

How much better is that than Cesalpino's sixteenth century idea that the seeds are produced by the transformation of the pith? Would it not be better to state the facts, without alleging that a "transformation" occurs in the leaves, etc., which exists only in our imagination?—C. R. B.]

CURRENT LITERATURE.

BOOK REVIEWS.

The botanists of Philadelphia.

AFTER much correspondence and research Dr. Harshberger has published, as a contribution to the history of botany in the United States, a bulky volume[1] comprising the biographies of the botanists who have lived in or near Philadelphia. The limit has a 60-mile radius, which is comfortably large, as it takes in the cities of Lancaster, Bethlehem, Reading, and Easton, Pa., most of New Jersey except the extreme northern part, and a good part of Delaware. Within this liberal area, a considerable number of people are included, whose title to be ranked as botanists of Philadelphia is slight, either because of their transitory interest in the subject or the brevity of their residence in the city. Philadelphia has had enough real botanists of her very own to make an interesting book about, and we could have spared the incidental collectors (like Josiah Gregg), the distinguished physicians (like Dr. Horatio C. Wood), and pharmacists (like Dr. A. W. Miller), who may well be astonished at being called botanists.

But inclusiveness is easier than exclusiveness, and if one can find the facts he wants, he may pass by the ones he does not want. The inaccessibility of data about the dead, and the indifference or modesty of the living constitute only a few of the difficulties to be overcome in getting up such a book as this. The compiler, therefore, deserves cordial recognition for his thankless task, and leniency for the shortcomings which are doubtless more evident to him than to others.

After a general introduction regarding the topography of the region, a sketch of the botanical development of the city is given. This is followed by the biographical sketches, often accompanied by portraits and more or less complete bibliographies. Besides these a long list is given of persons whose biographies were not obtainable, lists of the members of the Philadelphia Botanical Club, of the Botanical Society of Pennsylvania, of the Philadelphia Moss Chapter, a historical account of the scientific journals and serial publications issued from Philadelphia (19 in number), a description of Horticultural Hall in Fairmount Park, and sketches of trees of historical or botanical interest. — C. R. B.

[1] HARSHBERGER, JOHN W.: The botanists of Philadelphia and their work. 8vo., pp. xii + 457, *pl. 48*. Philadelphia: The Author. 1899. $4.00.

The economic products of plants.

A VERY important addition to the literature on economic botany is a book by Dr. A. E. Vogl dealing with the nutritive and otherwise useful vegetable products and devoted largely to describing the microscopic structure and examination of these substances.[2]

The author fully recognizes the fact that a thorough knowledge of general morphology should precede any attempt to obtain definite information concerning this special field, and the book presupposes some such knowledge.

The cereal flours and their preparation are first discussed. The chemical and histological characters of the different kinds of flour are stated and these used as the basis of excellent tests of identity and quality. Reduction of the quality by poor preparation, adulteration, substitution, or by the presence of certain fungi receives due attention. That part of this chapter which deals with starch and the leading starch producing plants constitutes one of the most interesting features of the book. Starch from a large number of sources is figured and the differences shown in the size, form, and structure of the grains. Though the drawings of these starch grains are somewhat schematic, they serve the author's purpose quite well. At the close of the section is a key intended to assist in identification under the microscope of various kinds of starch.

The second division of the book deals with vegetables. The treatment is brief and closes with an especially interesting discussion of the edible fungi. Because of the usual environment of the mushrooms, and since they are frequently inhabited by insects and larvæ which may secrete poisonous substances, Dr. Vogl thinks the desirability of using mushrooms as food is open to quite serious question. A good key for distinguishing the usual edible fungi from the poisonous ones is given.

The subject of fruits is treated briefly while the chapter on *narkotische Genussmittel* deals largely with tea and coffee. Tobacco is omitted from this chapter. A very extensive and comprehensive chapter on spices is followed by the closing chapter on microscopical tests for the chief adulterants of pulverized spices.

Throughout the book the author deals with the economic product in question rather than with the detailed taxonomy of the plant yielding the product, a very wise departure from the plan too often used in works on this and similar subjects. Much attention is given to the morphology and histology of the various vegetable products. The chemistry of some of the products is discussed, but it is to be regretted that this feature is not more full. The drawings are copious, mostly well-made, and nearly all of them new, some being of structures not previously figured.

[2] VOGL, A. E.: Die wichtigsten vegetabilischen Nahrungs- und Genussmittel. Pp. xv + 575. *figs.* 271. Leipzig and Wien: Urban & Schwarzenberg. 1899.

A very prominent feature of the book is the description and illustration of substances used in substitutions and adulterations. These substances are treated in connection with the article adulterated or substituted, and the means of detecting them are made so clear that they will doubtless prove of great assistance. This is certainly one of the best works published upon the morphology and histology of the vegetable food products, their substitutes and adulterants. — OTIS W. CALDWELL.

Letters of two botanists.

THE LIFE-LONG correspondence between Unger and Endlicher, the two great Austrian botanists of that classical time of botanical reconstruction in the third and fourth decades of the century, has fortunately been preserved, having been bequeathed by Unger's heirs to the Botanical Institute at the University of Graz. Dr. Haberlandt has published these letters in chronological order, beginning with the date November 10, 1829, and ending March 16, 1847, two years before Endlicher's death.[3] The letters are preceded by a general résumé of the historical content and significance of the correspondence. Ample footnotes furnish the reader with bearings on contemporaneous botanical history. Indeed, in the opinion of the reviewer, these constitute the most instructive part of the book. Such a grouping of historical facts about the lives of these two men revivifies the history of those decades of reawakening in a way that plain historical accounts cannot approach. It is the application of the newer methods of history to botany, and will be welcomed as such by students of the history of botany. The work ends with a detailed account of Endlicher's death, including letters from his attending physicians which effectually refute the belief, current everywhere for a half century, that Endlicher took his own life. This idea was so firmly established that it found expression in nearly all biographical notices of the time, in lexicons, cyclopedias, and even in Sachs' *History of Botany*. These letters here published for the first time leave no doubt in the mind of the reader that the death of the patient was natural, the result of disease attended by a long period of suffering.

A perusal of the letters themselves, while not adding much that is new to the history of botany, gives us an astonishingly deep insight into the intellectual workshops and the personal character of the correspondents. The letters which preceded the *Genera Plantarum* will be enjoyed by all systematists. We are permitted to see for the first time the "Unger-Endlichersche System" in its original form, and to observe it from its inception through its various modifications to the time of its publication. It seems that more is

[3] HABERLANDT, G.: Briefwechsel zwischen Franz Unger und Stephan Endlicher. 8vo. pp. v + 184. Two portraits and facsimiles of two letters. Berlin: Gebrüder Borntraeger. 1899. *M* 5.

due to Unger than the *Genera Plantarum* would lead us to believe. Unger was anxious to furnish floral diagrams for the entire work, and offered four drawings to Endlicher as models. Although they were mutually agreed on the plan, it was for some unknown reason abandoned, and this phase of systematic botany was thereby retarded a score of years; for it was not until the days of Eichler that floral diagrams of comparable excellence with those originals of Unger first made their appearance.

We are reminded, too, in these days of ecological enthusiasm that there is nothing new under the sun; for even as early as 1836 Unger was actively engaged in the study of the influence of soil and climate on the distribution of plants, regarding a floral region as "ein meteorologisches und geognostisches Gemälde." To use his words: "A floral picture should be drawn, which must not only show its individual parts in the relations of space and time, but also the causal relations between external factors and inner life should be studied." Unger is therefore to be regarded as one of the founders of the biological or ecological method in systematic botany.—EDWIN B. ULINE, *Mankato, Minn.*

New elementary text-books.

THE past few years have witnessed many notable advances in education, but none more remarkable than the wonderful improvement in the teaching of elementary botany, at least in its theory. From its prevailing state of well-nigh barren formalism of less than ten years ago, it has leaped forward until it has become a vigorous and sympathetic representation of the science. This progress has been both marked and stimulated by a series of noteworthy works, the latest and most advanced of which is Professor Coulter's *Plant Structures*.[4] Not only does this work mark the highest degree yet reached in books devoted to the newer mode of teaching the science, but it probably marks the highest point it will reach, for it represents very nearly or quite the logical extreme of the tendencies of recent years.

Any consideration of such a work as *Plant Structures* must take account of it from two points of view: first, its botanical merit, and second, its adaptability to the purposes for which it was prepared. As to the former, the present reviewer has little but praise. That the work would be quite in touch with the present state of knowledge, both in fact and in spirit, was of course to be expected of its author, and this expectation is fully justified by the book. It is not entirely free from errors, but these are so slight as to be inappreciable in the general excellence of the work. It is written with great clearness, illustrated fully and beautifully, and as a whole proportioned judicially. Whether viewed from a botanical, a literary, or an artistic standpoint the book is admirable.

[4] COULTER, JOHN M.: Plant structures, a second book of botany. Pp. x+348. *figs. 289.* New York: D. Appleton & Co. 1899. $1.20.

Passing next to consider its adaptability to elementary teaching, it becomes at once evident that the author's aim has been not only to meet the best conditions of the present, but to lead the teaching of the science into a better estate. As a work intended for use either now or in the future, by beginners, however, it seems to the present reviewer not free from faults. Some of the subjects particularly emphasized, especially the alternation of generations and the morphological transitions from group to group, though immensely important and full of meaning to advanced students, are too abstract to be of either much interest or profit to beginners, whose basis of fact is extremely slender. The treatment of these topics is particularly lucid, but one cannot resist the impression at times that Professor Coulter, in writing these parts, had his colleagues rather than his students in mind. For this reason the book would seem better fitted for the use of students of some maturity, and especially for those who already have studied botany to some extent, and who wish to go over the subject systematically.

Again, the treatment of physiology seems not only inadequate in relative amount, but also unfortunate in mode. The former point may be met if the student uses the companion volume *Plant Relations*, which contains considerable physiology; but probably most students, especially most school pupils, will use only *Plant Structures*. Several of the leading physiological topics are not only at least as illuminating as some of the morphological ones, which the author treats so well, but they are equally capable of laboratory study and demonstration. Indeed taking the two volumes *Plant Relations* and *Plant Structures* together, they appear to the present reviewer weak in their physiological parts, notwithstanding the immense importance of physiology as a basis for ecology. Moreover, physiology, taken in one mass by itself, as in *Plant Structures*, is apt to prove rather indigestible, and experience shows that its topics may be more profitably considered along with the structures in which the work is principally carried on. The morphology of the flower appears also to have received hardly adequate treatment, especially in view of the fact that it is a subject generally misunderstood by our teachers.

But these latter criticisms have to do more with matters of opinion than of fact, and opinions may well differ. Upon one point however we can all agree; that Professor Coulter has given us a most excellent book, and one that is sure to prove both stimulating and serviceable.— W. F. GANONG.

IN EVANS'S *Botany for beginners*[5] we have a handy little volume with some good points, but on the whole very crude. The plan of combining laboratory directions with reading text is not unwise, but the author has attempted to cover too wide a field. He is coerced, perhaps, by the English *bête noir*, the examinations of the Science and Art Department, and although

[5] EVANS, ERNEST: Botany for beginners. 12mo. pp. viii + 290. *figs. 271.* London and New York: The Macmillan Company. 1899.

he disclaims an intention to make a "cram" book, it is essentially that. The condensation, the selection of unsuitable and sometimes impossible material and subjects for beginners, the numerous errors of fact, and the crudity of many of the illustrations, some of which are utterly misleading, render the book valueless to teachers in this country. That it receives the hearty approval of a well-known English botanist in *Nature* indicates the wide divergence of standpoint in the teaching of botany in the two countries.—C. R. B.

TO THE multiplying list of American schoolbooks Dr. D. T. MacDougal contributes a modest little volume,[6] the most elementary of the recent ones, outlining "a study of the functions or action of the plants," whose "organs are considered chiefly as instruments for the performance of work, with but little attention to their morphology." The author thus depends upon the pupil's previous knowledge of the parts of plants, a knowledge which is amazingly scanty and inaccurate. However, by careful selection of topics and simple presentation, the author ensures the pupil, in the main, clear notions of the work that plants do.

But some topics are introduced in whose presentation the author is sorely hampered and of which the pupil is quite certain to get wry notions, because there is too little basal knowledge of the structures concerned. The most notable instance is in the section on "the way in which new plants arise," wherein the alternation of generations is discussed; a topic which the very elementary character of the book might well be held to preclude.

Nearly all the few defects of the book are chargeable to the striving after vividness, simplicity, and brevity, which are so dangerous yet withal so necessary in a book of this grade. That Dr. MacDougal has succeeded admirably no one who has tried to write a small and simple book will deny. We commend it to teachers who wish to interest pupils in plants at work.—C. R. B.

MINOR NOTICES.

AN elaborate monograph on the hemp, *Cannabis sativa*, by Briosi and Tognini, has been completed by the issue of the second part,[7] treating in minute detail and most thoroughly the internal anatomy, the first part being devoted to the flowers. The whole monograph, comprising 271 quarto pages and 49 plates, is a monument to the late Dr. Filippo Tognini and to his botanical master and associate, Dr. G. Briosi.—C. R. B.

[6] MACDOUGAL, D. T.: The nature and work of plants: an introduction to the study of botany. 12mo. pp. xviii + 218. New York: The Macmillan Company. 1900. 80 cts.

[7] BRIOSI, GIOVANI E TOGNINI, FILIPPO: Intorno alla anatomia della canapa (*Cannabis sativa* L.). Parto seconda; Organi vegetativi. 4to. Dagli *Atti* dell' Istituto Botanico di Pavia II. 4: 168–315. *Pl. 4–29.*

THERE APPEARED, in 1896, as the Fourth Memoir of the American Folk-Lore Society, a volume by Mrs. Fanny D. Bergen entitled *Current Superstitions*, dealing "almost entirely with beliefs not of a zoological or botanical nature." Mrs. Bergen has recently contributed to the Memoirs of the same society another volume comprising, as its name *Animal and Plant Lore*[8] indicates, only the folk-lore of animals and plants. This book will be especially interesting to those who have followed in the GAZETTE the same author's lists of the popular names of plants.

The table of contents of the second part, on plant lore, is at the outset instructive and interesting. There is a chapter on amulets, charms and divinations, another on omens, a third on weather signs, a fourth on folk-medicine, and finally one devoted to miscellaneous items which is no whit behind the others in curious and, to the scientific mind, astounding data. This folk-lore is furnished from a great many states, east, west, north, and south, and, as Professor Bergen suggests in his very interesting introduction, "if we cannot detect in it morsels from every country in Europe, from half the tribes of Africa, from a large part of Asia and the great Pacific islands, as well as from many tribes of American Indians, it is only because our analysis is not sufficiently minute."

As to amulets we find that nutmegs are regarded as a true panacea, being used to prevent boils, croup, neuralgia, cold sores (this latter in the neighborhood of Boston!) earache and sties. Mountain ash is used as a charm both of a good and bad nature, while dandelions and southernwood are prominent in processes of divination. The chapter on folk-medicine adduces many folk-remedies, which although probably the result of pure empiricism are not without foundation in fact; *e. g.*, the wide use of various parts of the elder, *Sambucus* sp. Extensive notes supplement the data given in the body of the book.

The value of the work done by Mrs. Bergen in collecting this material now can hardly be overrated. It is to be hoped that it may be continued until the annals of our American superstitions are fully recorded.—RODNEY H. TRUE.

THE TWO LATEST REPORTS of the state botanist of New York, Mr. Charles H. Peck,[9] are for the years 1897 and 1898. They are in the main

[8] BERGEN: Animal and plant lore, collected from the oral tradition of English speaking folk; edited and annotated by Fanny D. Bergen with an introduction by Joseph G. Bergen. Memoirs of the American Folk-Lore Society, volume 7. 8vo. pp. x + 180. Published for the American Folk-Lore Society by Houghton, Mifflin & Co., Boston and New York. 1899.

[9] PECK, CHARLES H.: Report of the State Botanist for 1897. Reprinted from *Fifty first Ann. Rep. of the N. Y. State Museum:* 267–321, *col. pl. A–B, 50–56 in 4to.* Albany, 1898. 10 cents.

PECK, CHARLES H.: Report of the State Botanist for 1898. *Bull. N. Y. State Museum* no. 25, **5**:619–688, *col. pl. 57–61 in 4to.* Albany, Oct. 1899. 40 cents.

similar to those which have appeared annually since 1868. Two decades of continuous and uniform labor, of the excellent quality shown by New York's official botanist, is a record of which to be proud.

Both these reports, like two of the preceding, have the plates in quarto form, but they may be once folded and conveniently bound with the text in an octavo volume. An innovation is introduced with the last report by having it issued in the series of *Bulletins* of the Museum, instead of being part of the *Annual Report*, as heretofore.

Each report contains notes upon a large number of species of flowering and cryptogramic plants of the state of New York, in part recorded for the first time as occurring within its limits. In the 1897 report twenty-five species of fungi are described as new, and six species in the 1898 report. The detailed account of edible fungi, with colored illustrations, is continued, twenty-three species being added in these reports. In the last report there is also an account of the plants on the summit of Mt. Marcy, whose height is 5344 feet.— J. C. A.

THE VOLUME of biological lectures given at the Woods Hole Biological Laboratory in 1898[10] contains addresses of zoological interest chiefly. Some of the sixteen lectures treat large problems, and therefore deserve the attention of botanists, though the treatment is strictly from the zoological standpoint. The address by E. B. Wilson on the structure of protoplasm, that by S. Watasé on protoplasmic contractility and phosphorescence, and that by T. H. Montgomery on various nucleolar structures of the cell may be named as of most general interest. The volume should be indexed.

THE ELEVENTH annual report of the director of the Missouri Botanical Garden has been issued.[11] Extracts of the most general interest have already been given. The scientific papers include H. von Schrenk's paper on an important disease of cypress timber and a similar disease in the wood of the genetically related Libocedrus; J. N. Rose's description of the four agaves which flowered in Washington in 1898, including a new species, *A. expatriata;* J. B. S. Norton's monograph of the North American euphorbias of the Tithymalus group, amounting to nearly forty species, and several new varieties, all of them figured on good plates; and J. G. Smith's revision of the half dozen United States Species of Lophotocarpus, together with a description of a new species of Sagittaria, *S. Eatoni.* The volume needs an index.

NOTES FOR STUDENTS.

EXPERIMENT STATION BULLETINS dealing with plant diseases, not heretofore mentioned in these pages, are as follows: A. P. Anderson (S. C. no. 41 : 3–14. *4 figs.*) describes "Rice blast and a new smut on the rice plant,"

[10] 8vo. pp. iv + 343, illust. Boston: Ginn & Co. 1899.

[11] 8vo. pp. 151, *pl. 58.*

the cause or causes of the first trouble being conjectured, and that of the second being identified as *Tilletia corona* Scrib.; while Ernest Walker in the same bulletin (p. 15–31, *1 fig.*) discusses "Treatment for rice smut," showing by tests that a number of fungicidal methods are available, but owing to failure in germinating the smut spores their efficiency was not determined. A. B. Cordley (Ore. no. 57 : 3–15. *1 pl. 7 figs.*) gives an account, under the title "Brown rot," of the injury to fruit in Oregon, due to *Monilia fructigena* Pers., together with a study of the fungus. H. H. Lamson (N. H. no. 65 : 99–108. *6 figs.*) gives "Notes on apple and potato diseases in 1898," with tests of fungicides. A. D. Selby (Ohio no. 97 : 31–61. *4 figs.*) presents considerable data upon smut, rust and scab of wheat and smut of oats. The Fusarium causing wheat scab has been traced to an ascigerous condition, believed to be identical with *Gibberella Saubinettii* Sacc. Results of treatment of seed grain to prevent the several smuts, J. F. Hickman being associated with this part of the work, are tabulated. A. D. Selby (Ohio no. 104 : 201–216. *3. pl.*) also shows the beneficial results obtained by spraying for peach curl, and gives a few notes on crown gall and yellows of peach. The same investigator (Ohio no. 105 : 217–235. *2 figs.*) publishes "Further studies of cucumber, melon and tomato diseases," with some account of the fungous and bacterial causes, and the results of spraying. F. A. Sirrine and F. C. Stewart (N. Y. no. 156 : 375–396. *4 pl.*) cover part of the same ground with statistics on "Spraying cucumbers in the season of 1898." A popular description of "The black rust or summer rust" of grains is given by Otto Lugger (Minn. no. 64 : 535–550. *13 figs.*) Methods for "The prevention of the smuts of cereal grains, and prevention of potato scab" are presented by H. L. Bolley (N. D. no. 37 : 363–379. *3 figs.*) with some results attained by farmers. H. Garman (Ky. no. 81 : 3–11. *2 pl. 1 fig.*) tells of "A method of avoiding lettuce rot" under glass by employing a system of sub-watering, and also gives the results of "Potato scab experiments made in 1898" in the use of fungicides. A. P. Anderson (S. C. no. 38 : 3–15. *5 figs.*) writes on "The asparagus rust in South Carolina," and G. E. Stone and R. E. Smith (Hatch, Mass. no. 61 : 3–20. *2 pl.*) write on "The asparagus rust in Massachusetts." J. C. Blair (Ill. no. 54 : 181–204. *27 figs.*) gives directions for "Spraying apple trees with special reference to apple scab fungus;" S. T. Maynard (Hatch, Mass. no. 60 : 3–11) provides formulæ for "Insecticides, fungicides," accompanied by a "Spraying calendar;" while W. M. Munson (Me. no. 52 . 3–8) gives general directions and formulæ for "The spraying of plants." A. L. Quaintance (Fla. no. 46 : 77–114. *12 figs.*) provides a rather full account of the strawberry thrips (*Thrips Tritici* Osb.) and of the onion thrips (*Thrips Tabaci* Lind,). and of the nature of the injuries they cause to plants. G. E. Stone and R. E. Smith (Hatch, Mass. no. 55 : 3–67. *12 pl.*) give a large amount of information about "Nematode worms" (*Hederodera radicola* Müll.), including historical and experimental data, much of it new, and with

illustrations showing the development of the worms and the production of galls on the plants. C. P. Close (N. Y. no. 161 : 153–164. *2 pl.*) records three season's tests in successfully combating gooseberry mildew with potassium sulfid, and less important results with Bordeaux mixture, lysol, and formalin. A popular two-page edition of this bulletin has been prepared by F. H. Hall.— J. C. A.

ANNUAL REPORTS of experiment stations published during the year 1899 not yet mentioned in these pages but containing matters of interest to botanists, may now be briefly noticed. In the nineteenth report of the New Jersey station B. D. Halsted (pp. 289–370, *12 pl.*) fills eighty pages with the results of a wealth of observation and experiment, supplemented with a dozen well printed plates. Lime is found to be effective in checking club-root (Plasmodiophora) of turnips, and sulfur ineffective; the latter, however, when applied to the soil outranked corrosive sublimate in reducing the scab of potatoes, and it is even more serviceable in case of sweet potatoes. The fungicides, Bordeaux mixture, cupram, soda-Bordeaux, and creolin, were used with varying results upon beans for *Colletotrichum lagenarium* Pass. and *Bacillus Phaseoli* Sm., on tomatoes for *Cladosporium fulvum* Cke., on spinach for a Cladosporium and a Phyllosticta, on egg-plants for *Phyllosticta hortorum* Speg., on cucumbers for *Colletotrichum lagenarium* Pass., and on beets for *Cercospora beticola* Sacc. Fungicides were also used on other plants with less conspicuous results. The smut of onions, *Urocystis Cepulæ* Fr., was introduced into a plat by bringing soil from another part of the state which had borne a smutted crop the year previous. There are observations upon asparagus rust, and on other parasitic fungi, on shading plants, on weeds, and on a number of other topics. The report closes with a discussion of the relation of fungi to weather.

In the eleventh report of the Hatch experiment station of Massachusetts, George E. Stone and R. E. Smith (pp. 142–167) record observations upon the occurrence and injury of Alternaria on muskmelon, rust on chrysanthemum, *Colletotrichum Violæ-tricoloris* on pansies, and of other parasitic fungi. Rather more space is given to physiological disorders of lilies, roses, cucumbers, and shade trees, being chiefly due to over feeding and to gas poisoning.

In the twenty-second report of the Connecticut station W. C. Sturgis (pp. 225–267) discusses the appearance and prevention of three melon diseases: wilt caused by *Bacillus tracheiphilus*, blight caused by *Alternaria Brassicæ*, and burn due to a sudden disturbance of equilibrium between water absorption and evaporation; of the mildew of lima beans and of the calico and spot diseases of tobacco. There are also seven pages of miscellaneous notes on plant diseases and spraying. In the same report E. H. Jenkins (pp. 310–316) gives statistics on the germination of garden seeds of various ages.

In the fourteenth report of the Maine station L. H. Merrill (pp. 64–74, *7 pl.*) reports in an interesting way upon box experiments with phosphoric acid from different sources. In the same report F. L. Harvey (pp. 131–135) has brief notes on weeds. Also W. M. Munson describes "The blueberry in Maine" (pp. 164–172, *2 pl.*), including four species, *Vaccinium Pennsylvanicum* Lam., *V. vacillans* Sol., *V. nigrum* Britt., and *V. Canadense* Rich., with notes on their culture; he reports experiments on "The acquisition of atmospheric nitrogen and soil inoculation" (pp. 208–212), and he has also a carefully prepared article on the behavior of pollen during fertilization and its after effects in formation of the fruit (pp. 219–229, *5 pl.*), which was in part presented before the Society for the Promotion of Agricultural Science at the Boston meeting in 1898. In the same report W. M. Munson and L. J. Shepard record experiments showing great superiority of crop from large seeds over small seeds of radish (pp. 158–160), and the conspicuous advantages of sub-watering over surface watering in growing radishes under glass (pp. 161–163. *1 pl.*).

In the eleventh report of the Rhode Island station Fred. W. Card (pp. 106–110, *7 pl.*) records the first season's results with apple trees having roots and branches pruned in various ways at time of planting. In the same report H. J. Wheeler and J. A. Tillinghast (pp. 122–191, *19 pl.*) give an interesting and instructive account of varied plat experiments in feeding plants and the use of "nitragin." In the same report J. A. Tillinghast (pp. 192–203) shows by statistics the effectiveness of the hot-water treatment of oats for smut, and the less value of the commercial "ceres pulver."—J. C. A.

BULLETINS from the experiment stations on medicinal and poisonous plants are as follows: C. W. Hyams (N. C. no. 150: 329–409) gives a list of over 800 species of wild plants of North Carolina having reputed medicinal virtues. They are arranged systematically under the Latin names, their poisonous or useful properties noted, and an index appended. It is a useful publication. B. D. Halsted (N. J. no. 135: 3–28, *4 pl. 2 figs.*) gives an account of the plants of New Jersey which are poisonous and liable to be eaten by men or animals, or are poisonous to the touch. It embraces much detailed and useful information. F. W. Morse and C. D. Howard (N. H. no. 56: 111–123, *6 figs.*) have investigated the "Poisonous properties of wild cherry leaves," testing the black cherry (*Prunus serotina*), choke cherry (*P. Virginiana*), and the red cherry (*P. Pennsylvanica*). All were found to be decidedly poisonous, the black cherry especially so. The youngest and most succulent leaves contain the most poison, which is increased somewhat by wilting, and partially lost by drying. The bulletin is an important contribution to our knowledge of the wild cherries. E. V. Wilcox (Mont. no. 15: 37–51, *3 pl.*) reports upon the poisoning of sheep by eating larkspur (*Delphinium Menziesii*), both unintentionally while grazing and experimentally by use of a fluid extract.—J. C. A.

MISS MARIA DAWSON has studied the tubercle organism and the mode of infection in *Vicia hirsuta* and *Pisum sativum*.[12] Her results confirm those of previous observers as to the mode of infection by tubes traversing one or more root hairs into the cortex. These tubes have the advancing end open and consist of numbers of straight rodlets with longer axes arallel to the line of growth of the tube. Finally, after traversing a cell, the tube bursts on one side and sets free the rodlets in the cell cavity. (No such infection tubes were found in Lupinus and Phaseolus.) The matrix enclosing the rodlets contains nothing of the nature of cellulose or chitin, or (probably) mucilage. These characters are conclusive against the organism being one of the true fungi, and call to mind Prazmowski's view that it is a filamentous zoogloea form of a schizomycete, and also Thaxter's Myxobacteriaceæ. Drop-culture experiments, the first of the kind, enabled the author to follow the multiplication of the rodlets by constriction and separation, the process being completed in 2–4 hours. Bacteroids were also developed in these cultures, but the author has not yet been able to observe the process of their development. Experiments were also made with "nitragin," which showed that it contained the tubercle organism and induced tubercle formation by direct application to seeds or through the soil.—C. R. B.

IN THE *Journal* of the Cincinnati Society of Natural History (**19**: 147–166. 4 Jan. 1900) Dr. A. P. Morgan publishes his fifth paper on the Myxomycetes of the Miami valley, Ohio, in which he presents various systems of classification of this group, some of them of only historical interest. The paper closes with his own grouping of the genera of North America, under four sections, with analytic keys to the genera.—C. R. B.

NO DOUBT students of histology will be interested in hearing how, according to the editor of *Meehan's Monthly*, trees increase in diameter. Explaining how a label was overgrown instead of being pushed outward he writes: "To those who understand the manner in which new wood forms, the explanation is simple. The increase in the girth of trees takes place during a few weeks at midsummer, and is by the rapid multiplication of minute cells. These, at first, are as soft as mush, and might be compared to the flow of so much yeast. If the flow is checked in one direction, it turns to the direction its neighbor is journeying, and adds itself to the volume of that stream." The persistence of erroneous ideas is amazing.—C. R. B.

STUDENTS of grasses will hardly look for articles on that group in the *Revue Bryologique*. Yet the opening number for 1900 contains two by N. Orzeszko of Nice; one on the processes for securing good sections of dried leaves of grasses, *i. e.*, for histological study of herbarium material, and a second consisting of an elaborate code of signs for histological description of

[12] Phil. Trans. Roy. Soc. London B. **192**: 1–28. 1899.

grass leaves. The former may be of some service; such schemes as the latter embodies are useful enough for the note book, but only cumber literature.—C. R. B.

OUR KNOWLEDGE of the life history of the Gnetaceæ has been considerably increased by Lotsy's[13] recent work on the life history of Gnetum. The difficulty in procuring material is responsible for the fact that comparatively few observations have been made. Of the three genera which compose the group, Welwitschia is found only in Damaraland, Ephedra is a desert plant, and the remaining genus, Gnetum, is found only in the tropics. Moreover, as in case of most gymnosperms, the collecting must extend over a considerable period in order to insure anything like a complete series of stages.

Dr. Lotsy's stay at the Buitenzorg botanical gardens in Java enabled him to secure a very complete series of stages in the development of *Gnetum gnemon*, from the earliest appearance of the flowers up to the formation of the embryo.

The inflorescences of *Gnetum gnemon* are spikes which come from the axils of opposite bracts. On each spike is a series of cups which owe their origin to a concrescence of bracts. At the base of each cup is a ring of tissue, upon the upper part of which may be seen a number of small, cone-shaped, greenish bodies; these are the female flowers. The mature female flower has three envelopes, which are formed in acropetal succession. The rudimentary female flowers found on the staminate spikes have only two envelopes.

The author regards the outer envelopes as whorls of bracts, which, for convenience, may be called the internal and external perianths. The inner envelope, which is longer and projects above the other two, he regards as an integument.

At the period of pollination a drop of fluid appears at the top of the integument, and consequently the term integumental stigma is applied. Pollination is probably effected by the wind, though it may be that insects have some part in it.

There is a pollen chamber at the top of the nucellus, formed by the degeneration of cells in that region. Before reaching the embryo-sac the pollen tube contains a tube nucleus and two generative nuclei. The details of spermatogenesis are reserved for a future paper. Each nucellus contains several macrospores which originate as in well-known gymnosperms. The early divisions in the macrospore do not seem to differ from those in Pinus or other familiar forms, there being first a series of nuclear divisions, so that a large number of nuclei lie free in the protoplasmic lining of the embryo-sac. The history from this stage differs from that of other gymnosperms. A constriction appears somewhat below the middle of the sac, reducing the lumen

[13] LOTSY, J.: Contributions to the life history of the genus Gnetum. Ann. du Jardin Bot. de Buitenzorg. II. 1: 46–114. *pl. 2–11.* 1899.

at this point, but by no means separating the upper and lower portions. Walls now appear in the lower portion so that it becomes filled with solid tissue at the apex of which bodies which may be rudimentary archegonia are sometimes found. In the upper portion the nuclei remain free in the protoplasmic lining of the sac.

At this stage, one or more pollen tubes enter, each bringing in two generative nuclei. Each generative nucleus fuses with one of the free nuclei in the sac, and the several copulation products become surrounded by denser protoplasm and soon acquire a membrane. They are now called zygotes. The zygotes germinate into long tubes, which grow down toward the base of the sac and penetrate the solid tissue there. Previous to this time this prothallial tissue has been increasing enormously and in the mature seed the fertile portion of the sac appears as a mere speck at the apex of it. At this stage the seed falls from the plant.

The development of the embryo from the tube which arises from the zygote has already been described by Bower.

The author suggests the following homology with the structures of the angiosperm sac.

Angiosperms		Morphological nature		Gnetum gnemon.
Egg apparatus	=	Archegonia	=	Fertile nuclei.
Micropylar polar nucleus	=	Prothallium	=	Sterile nuclei of upper part of sac.
Chalazal polar nucleus	=	Prothallium	=	Prothallium in lower part of sac.
Antipodals	=	Rudimentary archegonia	=	Rudimentary archegonia on lower part of sac.
Endosperm	=	Prothallium	=	Growing prothallium of lower part of sac.

The conclusion is reached that the Gnetaceæ are very ancient in origin and that they must have originated before or at the same time with gymnosperms (by this probably meaning the Coniferæ.)

He is inclined to regard "the Gnetaceæ as the equivalent of the gymnosperms and angiosperms combined and running parallel to these, having originated entirely independently of them. In these two parallel rows the gymnosperms may be compared to the Ephedroideæ and the angiosperms to the Gnetoideæ."

There will be objections to this interpretation if current views as to the geological history of the group are well founded.—CHARLES J. CHAMBERLAIN.

DATA bearing on the problem of the sexuality of the lichens are gradually accumulating, and the most recent contribution is by Darbishire[14] on *Physcia*

[14] DARBISHIRE: Ueber die Apothecienent wickelung der Flechte *Physcia pulverulenta* (Schreb.) Nyl. Jahrb. f. wiss. bot. **34**: 329. 1899.

pulverulenta. His investigations extend and support the results of Baur (1898). It will be remembered that Baur found again the trichogynes discovered by Stahl in members of the Collemaceæ, observed the sperms fused with their tips, and saw stages indicating that the trichogyne withered from above downward after fertilization.

Darbishire finds the archicarps each with its trichogyne in the youngest portions of the lichen thallus, and so very numerous that 700–1200 may be present on a small lobe. The lower part of the archicarp is an hypha of two or three loose coils, and is situated below the layer of algal cells about midway between the upper and lower surface of the thallus. The multicellular trichogyne extends as a filament between the algal elements to the exterior, where it projects above the upper surface. Sperms were observed attached to the tips of the trichogynes, but older stages show only one fused with each structure. When an archicarp of the group is fertilized it immediately develops rapidly, and, although others may show signs of fertilization and apparently start to develop, they finally disappear, and only one apothecium is formed.

After fertilization some of the large cells in the middle region of the coiled archicarp enlarge and finally fuse, so that there results a swollen multinucleate cell, the ascogonium, in each lobe of which lies a nucleus. A system of much branched hyphæ arises from the ascogonium, becoming the ascogenic hyphæ, from which the asci arise. The paraphyses develop from sterile hyphæ around, but entirely distinct from the ascogenic ones; the two systems of hyphæ being readily distinguishable. The further development of the apothecium follows closely the older accounts.

This investigation supports at all essential points the studies of Baur, and extends the evidence of sexuality to another family of lichens. It suggests the probability of the presence of trichogynes and the sexual act in many more groups than most botanists have been willing to admit in the past. In passing we should also note that the recent suggestion of Lindau in respect to the function of trichogynes appears very dubious. He has presented (1899) a theory that the trichogynes are organs whose function is to bore through the layer of algal elements to the surface of the lichen, thereby weakening this layer and allowing the apothecium to develop more readily and to push up from below. Darbishire shows that such a function for the trichogynes of *Physcia pulverulenta* is quite impossible, and that this operation is performed by the developing paraphyses.

We should bear in mind that whatever are the probabilities of sexuality among the lichens, we have not the knowledge that may be regarded as proof positive. We do not know the fate of the nucleus from the sperm, whether or where the fusion of sexual nuclei takes place, and withal we have a complexity of conditions in the multicellular trichogyne that is certainly very puzzling.—B. M. Davis.

A VERY clear paper by Dr. A. Nabokich, on the functions of aerial roots of orchids has appeared in *Botanisches Centralblatt* **80**: 331 *et seq.*, 1899. He shows that the supposed power of their velamen to condense water vapor from the atmosphere does not exist, and presents good evidence that these roots can make use of dew only as it condenses on leaves and stems and reaches them in drops. He proves that though they supply the plant with water, there is no correlation between transpiration and absorption, where there is storage of water. Absorption decreases with the temperature of the water, and when the storage factor was eliminated by the saturation of the tissue, there was little or no absorption in cold water if transpiration was prevented. He recognizes no relation between the presence of leaves with water storage and the presence or absence of velamen. The chief function of the velamen, he considers to be the protection of the parenchyma from sudden cooling at night, especially in the dry season, and in support of this view he lists nearly three hundred species showing the relation between the presence of velamen and the environment of the species. Those in moist, equable regions show at most only a few layers of the velamen, while those living under more variable conditions have from a few to eighteen layers. A second function of the velamen is the power of adapting the roots to hydrophytic conditions during the rainy season, when they are encased in water, and he believes the "white streaks" to be air reservoirs to allow them to breathe at this time.—L. M. SNOW.

UNDER THE title "The sexuality of the fungi," Harold Wager presents[15] a summary of the present knowledge regarding nuclear fusions in the fungi, and considers the leading interpretations which have been given to the facts. Wager regards it as possible that in Sphærotheca and similar forms the development of the ascogonial filament of cells exhausts the energy imparted by the preceding fusion of the antheridial and oogonial nuclei; that the energy necessary to produce another reproductive cell, the ascus, can only be obtained by a further nuclear fusion; and that in the higher Ascomycetes this second nuclear fusion has probably replaced altogether the morphologically sexual fusion of the simpler forms. This hypothesis may be extended to embrace the Ustilaginales and Uredinales.

It may well be that a deeper insight into sexuality itself and a due consideration of the later developments in physiology[16] will lead to views involving less of the idea of an energized nucleus.—F. L. STEVENS.

[15] Annals of Botany **13**: 575–597. 1899.

[16] LOEB, JACQUES: Am. Jour. of Phys. **3**: 135–138. 1899.

NEWS.

MR. WALTER R. SHAW has been appointed assistant professor of botany at Pomona College, Claremont, Col.

MR. A. I. ERIKSSON (Tufts College) has issued a catalogue of natural history books and authors' separates which will be of interest to botanists.

THE ANNUAL meeting of the American Association for the Advancement of Science will be held at Columbia University, New York, June 25–30, 1900. Titles and abstracts of botanical papers should be sent at once to the secretary of Section G, Dr. D. T. MacDougal, N. Y. Botanical Garden, N. Y. City.

ACCORDING TO the *Revue Bryologique* Dr. A. J. Grout, of the Boys High School, Brooklyn, N. Y., is intending to publish *exsiccati* of the pleurocarpous mosses of North America, "with the cooperation of the principal American bryologists." The first set, of twelve numbers, has just appeared. The price is to be $7.50 per century.

THE LAWRENCE SCIENTIFIC SCHOOL of Harvard University has issued a preliminary announcement of a four-year course in landscape architecture, including botany in the first year, horticulture in the second, a study of plants in relation to landscape planting in the third and fourth years, and the infirmities of plants in the fourth year.

THE FIFTH annual mid-winter meeting of the Vermont Botanical Club was held at the University of Vermont, January 26 and 27. Many papers of general as well as of local interest were presented and discussed. The following officers were elected: president, Ezra Brainerd; vice president, C. G. Pringle; secretary and treasurer, L. R. Jones.

PROFESSOR RYŌKICHI YATABE, founder of the Botanical Society of Japan, and for ten years its president, was drowned September 10, 1899, at Kamakura, where he was spending the summer. He studied in America and was the first professor of botany in the Imperial University of Japan. The December number of the Tokyo *Botanical Magazine* contains a fine portrait of him.

DR. N. L. BRITTON asks the BOTANICAL GAZETTE to announce that pressure of work during the latter part of last year made it impossible at that time for him to bring his address as retiring president of the Botanical Society of America into satisfactory form for the usual publication. The

substance of the address, however, will appear in *Bulletin no. 5* of the New York Botanical Garden, now in press.

WITH THE conclusion of the seventh volume, December 1899, M. Eugène Autran announced that the publication of the *Bulletin de l'Herbier Boissier* terminates. It will be welcome news to taxonomists, who have learned to look to the *Bulletin* for work of the highest quality, that a successor has already appeared in the *Mémoirs*, having much the same form, but consisting of a series of separate papers issued at irregular intervals.

PRESIDENT HADLEY has made the welcome announcement that a school of forestry is to be established at Yale University. It is promised that the "principles of botany" are to form an important part of the instruction. It would be most gratifying to botanists if the science in its modern aspects and development should be fully presented at Yale, which, in this particular, has long lagged far behind most western institutions and her great New England rival, Harvard.

THE FIRST number of the *Journal* of the New York Botanical Garden was issued with the beginning of the year. It is an interesting 16-page number, with a late photograph of the museum building as a frontispiece. The *Journal* is to be edited by Dr. D. T. MacDougal, and will be published monthly, containing illustrated non-technical articles, news, notes, etc., of general interest. The publications of the Garden now comprise four series: the *Journal*, the *Bulletin*, the *Memoirs*, and the *Contributions*, the latter including reprints from publications other than the first three. Such multiplication of titles is unfortunate, because it increases the chances for error in citation and the labor of keeping track of publications. The Garden is following the bad example of some older institutions in this respect, notably the Buitenzorg Garden, which has recently established the *sixth* series of its publications. We wish the New York Garden would lead a reform in this respect.